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Behavior, Energetics, And Swimming Performance Of The American Paddlefish, Polyodon Spathula, In A Lower Mississippi River Oxbow

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BEHAVIOR, ENERGETICS, AND SWIMMING PERFORMANCE OF THE AMERICAN PADDLEFISH, *POLYODON SPATHULA*, IN A LOWER MISSISSIPPI RIVER OXBOW

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ABSTRACT

Paddlefish often frequent oxbows and backwater habitats between periods of migration. Speculation as to the use and energetic savings associated with this seasonal residence has not been substantiated. This study used radio telemetry to track the seasonal movements and swim tunnel respirometry to estimate metabolic rates and swimming efficiency of paddlefish within an oxbow located just north of Clarksdale, Mississippi (Moon Lake). Paddlefish overwintered in the deepest portions of Moon Lake with little movement into shallower areas. Paddlefish swimming performance was measured at four swimming speeds (76.04, 91.27, 106.50, and 121.72 cm/s) to determine the cost of locomotion over season as measured by oxygen consumption and reported as the cost of transport: cost in calories to move one gram of body mass one kilometer. The optimal swimming speed (U_{opt}), the swimming speed at which the cost of transport is the lowest, for any given month (January, February, May, and September) was between 106.50 and 121.72 cm/s and was estimated to be 0.078 calories/g/km for February, May, and September, and 0.045 calories/g/km in January. The caloric availability within the lake was monitored by zooplankton sampling to determine the potential energetic gain from paddlefish filter feeding. The ratio of calories expended to calories gained (cost to benefit ratio) was calculated for each of the four swimming speeds tested during swimming trials. The cost-to-benefit ratios in January and February were less than 1 at all speeds tested and suggested that paddlefish swimming efficiency was high and zooplankton abundance was adequate to support energetic gain. The most efficient swimming speed during January and February was 121.17 and 91.27 cm/s, respectively. Cost-to-benefit ratios in January and February were 0.20 and 0.50 cal/g/km, respectively. Costs began to

exceed benefits in May and September as zooplankton densities dropped drastically. This was evidenced by the decline in average caloric value of lake water (29.89 and 4.79 calories/cubic meter for May and September, respectively. In September the cost of locomotion was around 200 to 400% of benefit. The significant drop in zooplankton may have cued paddlefish to move out of Moon Lake.

DEDICATION

I would like to dedicate this work to my father and mother, Bob and Dorothy Cage, for their constant encouragement throughout my academic career. I love you dearly.

LIST OF ABBREVIATIONS AND SYMBOLS

ATP	Adenosine Triphosphate
COT	Cost of transport
DV	Displacement Volume
ECZS	Energetic Content of Zooplankton Samples
ED	Energetic Density
FG	Fast Glycolytic
FOG	Fast Oxidative Glycolytic
FLC	Fish Locality Coordinates
GFB	Gonadal Fat Bodies
IoT	Internet of Things
MH	Mouth Height
MW	Mouth Width
RGC	Randomly Generated Coordinates
SO	Slow Oxidative
STDW	Sample Total Dry Weight
SV	Settlement Volume
TEC	Total Energetic Density
TNOC	Total Number of Organisms per Category
TNOT	Total Number of Organisms per Tow

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Brown, John Norton, and Cameron Sims, formed a formidable field crew with an endless committment to excellence. Their diverse personalities and charming wit cultivated a wonderful environment of comraderie, laughter, and work ethic. It was a great to work with them daily.

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CHAPTER I

GENERAL BACKGROUND

1. Introduction

Success, in biological terms, is the proliferation of a species over generations. With reproduction acting as "the strongest biological imperative" (Sapolsky, 2002), life history strategies have evolved to maintain homeostasis and to maximize growth and reproduction. Fish consume energy in an effort to meet the demands for maintenance, activity, growth, and reproduction (Tytler and Calow, 1985). Metabolism is the sum of all biochemical reactions occurring in an organism and provides the energy, in the form of adenosine triphosphate (ATP), necessary to support cellular processes (Kitchell, 1983; Tortora and Derrickson, 2009). In a basic energy budget,

$$_{p}Q_{R} = Q_{S} + Q_{L} + Q_{G} + Q_{P}$$

$_{p}Q_{R}$ is the proportion of food ration that can be digested, absorbed, and utilized for energy production (Webb, 1978; Diana, 1995). The net energy left for standard metabolism (Q_S), locomotion (Q_L), growth (Q_G), and reproduction Q_P is the difference between the total food intake (Q_R), minus the energy lost to waste, which includes indigestible material (Q_F), excretion of ammonia (deamination of amino acids) (Q_N), and the energy lost as heat (Q_H). Stated another way:

$$_{p}Q_{R} = Q_{R} - Q_{F} - Q_{N} - Q_{H}$$

where ${}_pQ_R$ is termed the assimilation efficiency and varies with diet, particle size, and temperature (Winberg, 1956; Webb, 1978; Diana, 1995). Heat increment (Q_H) accounts for both metabolic heat loss and the cost of digestion (specific dynamic action) or SDA (Brett, 1964). The sum of waste as excretion, feces, and SDA are a function of feeding rate (Elliott, 1976), but often represent fractional proportions of total diet (Kitchell, 1983). The remaining energy can be allocated for standard metabolism (Q_S), locomotion (Q_L), growth (Q_G), and reproduction (Q_P), respectively (Webb, 1978; Brett and Groves, 1979; Diana, 1995).

Many continuous swimmers have evolved an "energetically speculative" strategy with a high investment in activity (Stevens and Neill, 1978). They optimize the coefficient of caloric expenditure ($Q_S + Q_L$) to caloric intake (Q_R) leaving surplus for growth and reproduction. The behavioral changes that affect these variables are important aspects of energetic optimization. Combinations of weather patterns, habitat use, swimming preference, prey abundance, and feeding interval may have varying effects on energetic input/output with the assumption that deliberate changes in paddlefish behavior will optimize the balance between costs and benefits. The coefficient of energy expenditure to energy consumption is maximized in continuous swimmers, such as ram ventilators, and often optimization involves extrasensory components (Weihs and Webb, 1983). Feeding metabolism is the energy invested in searching and consuming potential energy from prey (Brett and Groves, 1979; O'Brien, 1979; Weihs and Webb, 1983). Paddlefish possess electrosensory capabilities as provided by the Ampulla of Lorenzini replete upon the dermal surfaces of their paddle-like rostrum and operculum (Chagnaud et al., 2008). Wilkens and Hofmann (2007) have shown that such sensory components enhance prey encounters, thus, reducing energy expenditure (Wojtenek et al., 2001; Wilkens and Hofmann, 2007).

Simply, the balance of energy within a system, is based on a fish's biological framework – the set of morphological, physiological and biochemical traits of the particular species (Claireaux and Lefrançois, 2007). Through genotypic and phenotypic expression, fish respond to environmental variation (i.e. temperature, dissolved oxygen, stress) within biological boundaries and on multiple levels of organization (Fry, 1971; Weihs, 1973, 1975; Weihs and Webb, 1983; Hochachka and Somero, 1984). Behavior, habitat selection, and variation in life history patterns are often a direct response to short-term and long-term environmental perturbations (Brett, 1956; Rodgers, 1998; Claireaux and Lefrançois, 2007).

It is the adaptation to habitat that evolutionary physiologists try to evaluate to provide an index of fitness. The effects of environmental variability on activity, performance, and behavior are dynamic, complex, and often unpredictable. In as much, estimates of these effects on fish production are limited. Mathematical models are often incomplete and experimental designs often fail to replicate the natural heterogeneity of complex systems (Neill et al., 1994; Van der Veer et al., 2000; Claireaux and Lefrançois, 2007). Therefore, it is the purpose of this research to begin to understand how the ecology of paddlefish and zooplankton affect paddlefish bioenergetics and distribution within an oxbow lake in northwest Mississippi.

The paddlefish, *Polyodon spathula*, (Polyodontidae: Actinopterygii) is arguably the most distinct of the North American fishes, possessing an extended paddle-like rostrum with electroreceptor capabilities (Wilkens et al., 2002). The paddlefish's biological framework poses unique and interesting challenges for homeostatic balance. Paddlefish are obligate, ram ventilating, filter feeders. Ram ventilators regulate gill ventilation and metabolic demand through adjustments of mouth gape and swimming speed (Parsons and Carlson, 1998b) to adequately flush oxygen over the gills. As suspension feeders, ram ventilation and prey filtration interact

and may impede gill ventilation. Paddlefish possess a distensible jaw and buccal cavity that inflates during feeding. The increased drag and elevated energy expenditure with suspension feeding produces an energetic conundrum requiring paddlefish to moderate both swimming speed and buccal water velocity (Cech and Cheer, 1994). The caloric value acquired from feeding must be great enough to offset the cost of swimming (both cruising and suspension feeding). This phenomenon can be exacerbated with changes in water temperature, fish size, and seasonal changes in swimming performance. It has been suggested that a paddlefish's rostrum counteracts the drag incurred while swimming with the mouth agape, by providing lift.

A majority of the cost to paddlefish comes from locomotion. Environmental conditions such as temperature (Moore, 1973; Wardle, 1980; Adams and Parsons, 1998), oxygen tension (Fry, 1971; Carlson and Parsons, 2001), photoperiod (Smiley and Parsons, 1997), water depth (Rodgers, 1998), turbidity (Gaston, unpublished data), as well as, biological factors including size, gas transport and exchange, nutrient transport, and level of activity (Webb, 1975) influence swimming potential. Of these, temperature is considered the most pervasive, playing an important role in regulating swimming performance, in part, by affecting oxygen solubility and regulating metabolism (Diana, 1995; Jobling, 1995).

The overall objective of this work was to determine factors that influence the relationship between energy loss through locomotion and energy gain through prey consumption (cost-to-benefit ratio) in paddlefish. The approach had three parts: 1) estimate the energy acquired ("benefits" in cost/benefit ratio) as caloric intake from potential zooplankton prey (chapter 2), 2) determine the relationship between locomotion (swimming speed) and energy expenditure (chapter 3) and 3) document the daily paddlefish activity ("costs" in cost/benefit ratio) through

measures of total swimming speed to estimate energetic costs of daily movements (chapter 4 & 5).

Chapter two examines the effects of photoperiod and season on zooplankton abundance and composition. These values represent the denominator of the cost-to-benefit ratio. Zooplankton sampled over a twenty-four hour diel cycle from January to September of 2014 were examined to determine energy content (calories/gram). The objectives were to: 1) determine the net caloric value of zooplankton over season, 2) record changes in the abundance and composition of zooplankton over season, 3) determine the relationship of gross caloric value (total calories per sample) with changes in abundance and composition over season, and 4) determine the relationship between nutrient availability (due to changes in zooplankton abundance and composition) and changes in swimming behavior and habitat use of paddlefish.

Chapter three describes the methods of quantifying swimming expenditure of paddlefish by testing the swimming performance of individuals sampled from a small population residing in Moon Lake, a small oxbow in northwest Mississippi. It is assumed that the largest costs to paddlefish are changes in seasonal swimming performance as related to temperature. Metabolic rates of locomotion were estimated using a large portable swim tunnel respirometer with the intent to determine the relationship between swimming speed and energy expenditure by proxy of oxygen consumption. Metabolic rates were measured as oxygen consumption over time and were converted to caloric expenditure as a function of swimming performance and body mass (kg). Expenditure estimates were used to calculate the cost of transport (calories $gram^{-1}$ $kilometer^{-1}$) of paddlefish as a function of season and comparisons with other species with similar physiology were noted.

Chapter four provides a technical analysis of the speed sensing instrument. Understanding the relationship between energy expenditure of free-ranging paddlefish and the ecology of their prey (zooplankton: Copepods and Cladocerans) provides insight into the daily energetic strategies that paddlefish may employ to optimally feed in order to maximize growth and reproduction. An overview of the technical specifications, device calibration, software, code samples, and a list of hardware components for this new device are provided.

Fish movement and swimming behavior were monitored in-situ with radio telemetry to determine relationships between swimming patterns, prey dynamics, and habitat use (chapter 5). The correlation between daily activity (energetic cost) and zooplankton distribution provided insight on how habitat use in paddlefish reflected feeding optimality (cost-to-benefit ratio) in occurrence with changes in zooplankton caloric value and dispersal. Such information provided a useful measure of the caloric threshold relative to swimming performance and changes with season. Using a device newly developed in this study for measuring swimming speed (chapter 5), along with recording geographical movements through telemetric tracking, an assessment of feeding optimality (cost-to-benefit ratio of locomotory expenditure to caloric availability through suspension feeding) was addressed as it pertains to paddlefish bioenergetics and movement from Moon Lake.

2. Focal Species

Paddlefish range in North America from the upper Missouri River in Montana and North Dakota to the Ohio River Valley, while their southern expansion is in the Mississippi River and its tributaries and reaches to the Gulf of Mexico (Jennings and Zigler, 2009). Paddlefish have evolved within temporally and spatially divergent habitat patterns and have learned to use this patchwork to complete their life cycles (Braaten et al., 2009). Swimming, feeding, and

reproductive behavior reflect local variation in spatial diversity, food availability, and environmental cues, but share common elements (Smith et al., 2009). Paddlefish are long-lived species living up to thirty (30) years and reaching lengths and weights of over 2.2 meters and 72 kg, respectively. Compared with other freshwater species, sexual maturity is delayed in paddlefish and disparity in age and spawning frequency occurs between the genders (Jennings and Zigler, 2009). Females spawn every few years, but are relatively fecund (9,000 – 26,000 eggs). Egg size ranges from 2.0 to 4.0 mm in diameter and optimal development occurs at a temperature of 18°C, but seems to vary with locality and drainage (DeVries et al., 2009; Jennings and Zigler, 2009).

Paddlefish spend much of their time in main channels of large rivers seeking pockets of reduced flow at river confluences and deep water eddies (Braaten et al., 2009). Paddlefish diets consist mainly of cladocerans and copepods, but fluctuate with shifts in local fauna and densities. Many investigators have reported paddlefish to be opportunistic when their main diet is scarce, feeding on midge flies, and small fish (Rosen and Hales, 1981; Hageman et al., 1986; Hoxmeier and Devries, 1997; Smith et al., 2009). Oxbows and lacustrine floodplains, rich in food resources and accommodating current, facilitate early growth and juvenile survival, but may risk entrapment during intermittent disconnection with main river channels (Hoxmeier and Devries, 1997). Flow pulse, temperature, and photoperiod are cited as environmental cues triggering paddlefish spawning migrations and temporal and geospatial differences which occur between populations (O'Keefe and Jackson, 2009).

CHAPTER II

SEASONAL DIFFERENCES IN PLANKTON COMPOSITION AND NUTRIENT VALUE IN A LOWER MISSISSIPPI RIVER OXBOW, MOON LAKE, MISSISSIPPI

1. Introduction

Branchiopoda (Cladocera) and Copepoda are two of the most prevalent and widely distributed Crustaceans in North American freshwaters (Thorp and Covich, 2001). Scientists estimate there are over 700 species inhabiting freshwater environments (Thorp and Covich, 2001). Cladocera, including the common "water flea", *Daphnia,* along with the two major groups of Copepoda, Calanoidea and Cyclopoidea, represent over 50% of some freshwater zooplankton lacustrine communities and are a major staple in food web stability (Thorp and Covich, 2001). Both groups are important prey items for fishes and other aquatic predators constituting up to 97% of the total diet of some freshwater fishes (Smith et al., 2009).

Copepods and cladocerans are a rich energy source for planktivores and often increase in body mass and nutrient richness due to periods of cyclomorphosis and optimal grazing. Flat bodies increase surface area and exaggerated appendages trap oil to promote stability within the water column and enhance buoyancy. Such adaptations increase the nutrient value for predators, as larger, lipid rich prey items provide a higher caloric content per unit mass (Redden et al., 2009). Predatory behavior and feeding effort may shift, commensurate with seasonal changes in energetic capacity of selected prey, reflecting both short- and long-term swimming patterns (Jobling, 1995; Dodson and Frey, 2001). Diel patterns of oxygen consumption have been reported for several species of zooplanktivores (Lui et al., 1997; Xu et al., 2009). Xu et al.

(1997) found that peak oxygen consumption in paddlefish (O_2 g^{-1} h^{-1}) occurred at 6:00 a.m. and 8:00 p.m. suggesting that their natural circadian rhythms may reflect peak feeding times that coincide with zooplankton vertical migration and prey abundance.

Classified as mesoplankton, cladocerans and copepods range in size from 0.1 to 2.0 mm and demonstrate a crepuscular migration, rising to the surface to graze on phytoplankton shortly after dusk, and returning to deeper sanctuary slightly before dawn (Dodson and Frey, 2001; Williamson and Reid, 2001; Redden et al., 2009). Gender and age are often factors affecting migration and column composition and will vary with season and habitat type. The upper and lower bounds of the migration zone fluctuates seasonally, as light attenuation varies with photoperiod and temperature limits metabolic activity (Kerfoot, 1970; Van Gool and Ringelberg, 1998; Redden et al., 2009). Although many authors cite avoidance of predators as the relevant factor for vertical migration, such migrations are essential for proper maintenance and optimization of growth, reproduction and fecundity (Loose, 1993; Dodson and Frey, 2001).

Fluctuations in the caloric availability within a system are important in the energetic balance in bioenergetics and paddlefish activity. Decreases in nutrient availability have the potential to slow growth and reproductive output. The total caloric value of prey is a product of zooplankton abundance and the basal caloric energy of prey items, and provides a gauge of the top-down energy available to zooplanktivores within an enclosed water basin. The average calories per gram may vary with species, time of day, and season.

The objectives of this chapter are: 1) to determine if paddlefish have the ability to detect and exploit dense patches of zooplankton with high caloric content, 2) to test for daily and seasonal differences in zooplankton composition, abundance, and caloric value, and 3) use the average caloric concentration of zooplankton each month in an analysis of feeding optimality as

measured by the ratio of the total caloric expenditure of locomotion to the total caloric value obtained by a filter feeding paddlefish (cost-to-benefit ratio). The methods for estimating the total caloric value filtered by a paddlefish during a given season is located in the material and methods in chapter three under the title: calculating energetic benefits (calories) of filtering paddlefish. The relative abundance, composition, and caloric value between patches sampled from areas where paddlefish were located was compared with areas sampled randomly throughout the lake. Likewise, concurrent daily and seasonal shifts in total caloric value, species composition, and zooplankton abundance was also compared.

2. Materials and Methods

Zooplankton Sampling

Zooplankton collections were taken simultaneously during telemetry tracking trips between January 1st and September 17th of 2014. Each tow event consisted of a single ten-minute sampling tow using a General Oceanics plankton net (0.50 m opening, 153µ mesh, 5/1 length to mouth ratio) and digital flowmeter with standard rotor odometer. Sample tows were taken at one of two categorical locations: 1) fish locality coordinates (FLC) and 2) randomly generated coordinates (RGC) within Moon Lake. Time of day was divided into two categories: day (0500 to 1659), and night (1700 to 0459). An attempt was made to collect equivalent samples representative of each period.

Random coordinates were generated using ArcGis® ArcMap™ software. Zooplankton tows were sampled within a meter of the surface and approximately 50 feet behind the boat, well outside the influence of the boat's wake. Collected zooplankton were stored in gallon-sized Ziploc® freezer bags filled with lake water, stored on ice, and later held at -80°C in the laboratory.

Zooplankton Metrics

Frozen content was thawed, rinsed, and filtered using a Fisher Scientific, 125μm U.S.A standard testing sieve. Zooplankton was suspended in distilled water within a graduated cylinder and filled up to a 250 ml volumetric mixture. One hour was allowed for zooplankton to settle before recording the approximate settlement volume (SV) to the nearest milliliter. The supernatant was poured into a second 250 ml graduated cylinder. The volume of the water column was recorded and subtracted from 250 mL to provide a measure of the zooplankton volume displaced (DV) in milliliters. Zooplankton was re-suspended into a 250 ml graduated cylinder and serially split into an appropriate size using an 1831-F10 Folsom Plankton Splitter. The extracted zooplankton subsample was re-suspended into a 25 or 30 ml graduated cylinder. Following a brief agitation to circulate zooplankton, 2 to 10 mL were placed into a Ward Counting Wheel, identified to the lowest taxonomic group using keys from Thorp and Covich (2001), and enumerated to provide an estimate of the total number of organisms per category (TNOC) and total number of organisms per tow sample (TNOT). Composition and density were calculated, respectively, using Microsoft Excel®.

Analytical Procedures

An oxygen bomb calorimeter (Parr model 1266) was used to determine energetic content of the zooplankton samples (ECZS) by determining the energetic density: the energy per unit weight of plankton measured in calories per gram. The majority of moisture was removed before recording an initial weight. Zooplankton samples were placed onto an aluminum drying tray and placed into a heating oven (~40°C) until a constant weight was achieved. This was recorded as the sample total dry weight (STDW). One to three dried pellets were constructed (based on

availability), weighed and burned in the oxygen bomb calorimeter to determine energetic density in calories per gram (ED).

The total energetic content (TEC) in calories of each tow net sample was determined by multiplying the average of the three calorimetry runs by the (STDW) using the following computation: TEC = average energetic density in cal/g x STDW. Estimations of the volume of water (cm^3) sampled during each tow was calculated as follows: π x (net diameter) ^{2} x distance / 4. The total distance towed was calculated by the following formula: distance = (odometer 1 – odometer 2) x 26,873) / 999999. The odometer readings were taken from the General Oceanics digital flowmeter at the beginning and at the end of each tow event. The standard rotor constant (26,873) was provided by General Oceanics documentation at: http://www.sluse.mju.ac.th/database/silo/otherpub/2030flowmetermanual.pdf. These parameters were used to calculate the average calories per meter of water sampled and the energy per cubic meter. Compared with the cost of transport, calculated from chapter 3, the cost-to-benefit analyses were addressed.

Statistical Analysis

An initial two-way ANOVA was used to test for differences in the average calories per gram zooplankton between two groups with variable zooplankton compositions: those samples with cladocerans making up more than 75% of the composition and those samples with cladocerans making up less than 75% of the composition. Subsequent two-way ANOVA's were used to test for differences in calories per cubic meter across season between samples taken during the day versus night, and samples taken in areas of fish presence versus randomly sampled areas of the lake. A Kruskal-Wallis one-way ANOVA of ranks was used to test for differences in biomass (mg/m^3) between months.

Prior to using the two-way ANOVA's a Shapiro-Wilk Test for Normality was applied to all data sets to test for the assumption that data were normally distributed. Data sets that were not normally distributed were log10 transformed. Levene's Test for Homogeneity of Variance was used on all data sets to determine if groups met the assumption of equal variance.

3. Results

Temperature

Water surface temperature from January to September of 2014 ranged from 0.40°C and 29.33°C, respectively (Table 1). Samples were grouped for January to February, March to April, May, and July to September to maximize samples per temperature regime.

Zooplankton Density, Composition, and Biomass

Cladocerans and copepods were the largest constituents of zooplankton samples with the "water flea" (Cladocerans) comprising the majority. Percent composition over the entire data set was comprised of Cladocerans (71.25%), [Copepods (Cyclopoids (13.78%), Calanoids (12.61%)], and other (2.36%). Water mites (Family Hydrachnidiae), fish louse (genus *Argulus*), ostracods (Class Ostracoda), Chironomids (Family Chironomidae), and Chaoborus (Genus *Chaoborus*) were grouped in the other category. *Chaoborus* was the most prevalent of these and both larval and pupae forms were found during the study period. The average composition by month is listed in Figure 1.

Zooplankton abundance showed a steady increase from February ($\bar{X}$ = 2203.82 org/m^3) to April ($\bar{X}$ = 7433.56 org/m^3) before a sharp decline in May ($\bar{X}$ = 1721.69 org/m^3) and September ($\bar{X}$ = 171.53 org/m^3). Cladocerans and Copepods made up the majority of the composition during all months sampled (Figure 2), with the two groups evenly represented during February (Cladocerans: 48%; Copepods: 51%). Cladocerans constituted the highest percentages in March

Table 1. Water Surface Temperatures by Months

	Jan-Feb	Mar-Apr	May	Sept
Minimum	0.40	12.40	20.06	25.00
Mean	2.49	15.31	21.39	26.02
Maximum	3.38	21.40	22.94	29.33
Range	2.98	9.00	2.88	4.33

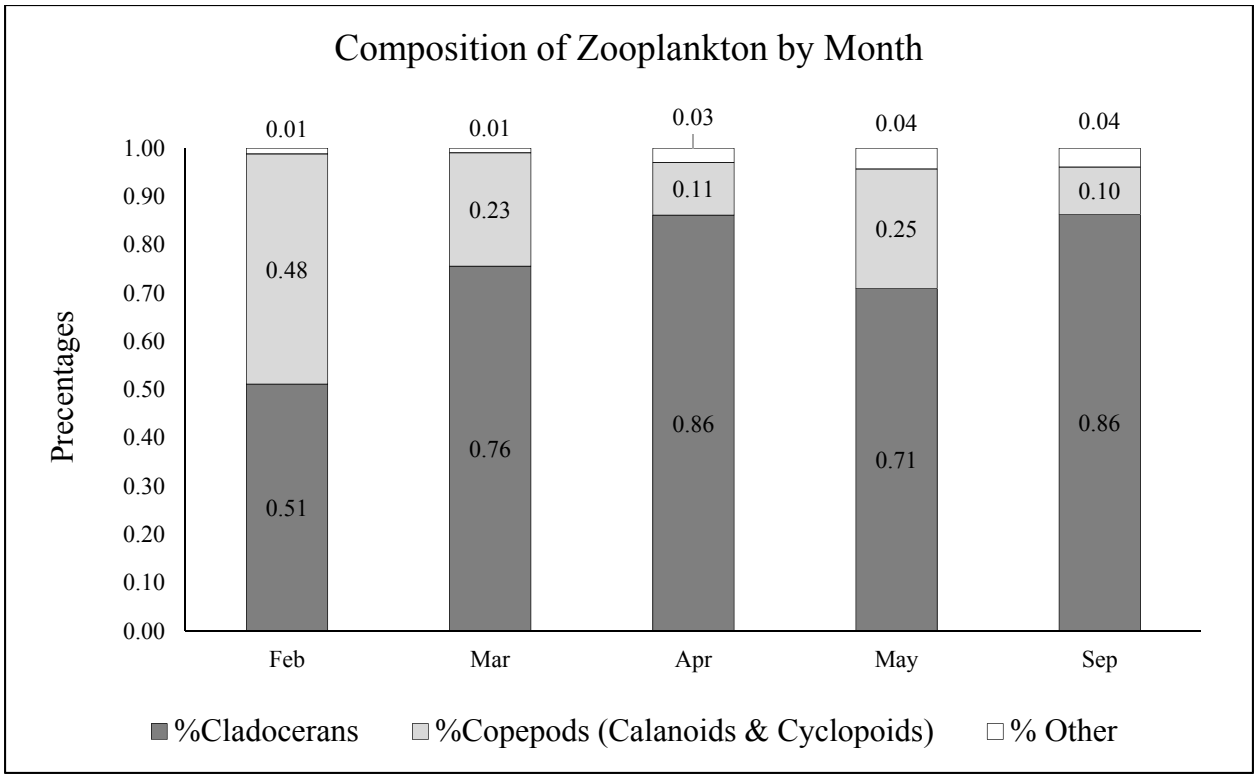

Figure 1. Composition of zooplankton by month

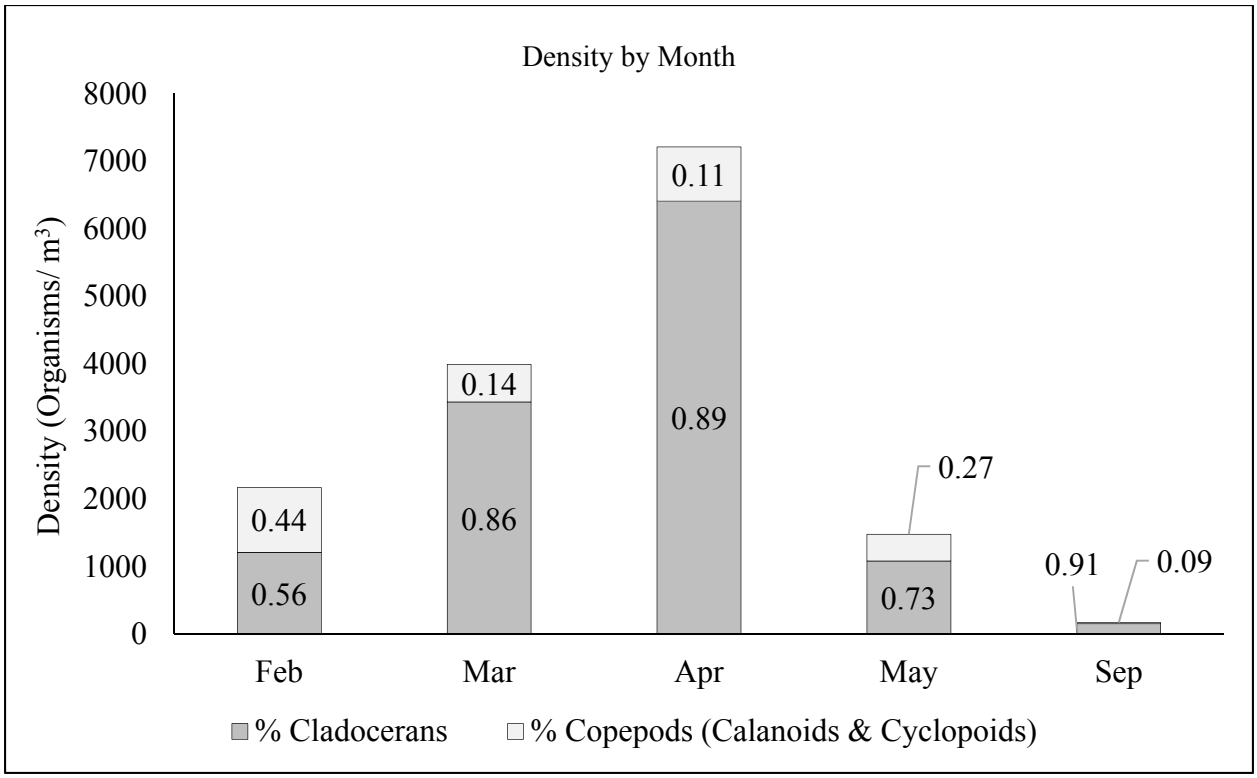

Figure 2. Total abundance and proportion of cladocerans to copepods by season

(86%), April (89%), May (73%), and September (91%). The calories per gram of zooplankton was highest in February when Cladocerans represented less than 75% of the sample composition ($\bar{X}$ = 5271.39 cal/g) as opposed to warmer months when Cladocerans represented greater than 74% of the species composition ($\bar{X}$ = 4727.20 cal/g) (Table 2). The mean calories per gram zooplankton (Table 3), however, did not differ significantly with composition ($_{ANOVA}$ $F_{1, 35}$ = 1.74; p = 0.196) or across months ($_{ANOVA}$ $F_{1, 35}$ = 0.02; p = 0.88). Both biomass (mg/m^3) and caloric concentration (cal/m^3) were significantly different across months using a nonparametric independent samples Kruskal-Wallis one-way ANOVA (p = 0.0001; α = 0.05) (Figure 3; Figure 4).

Zooplankton Caloric Value: Day vs. Night

A two-way ANOVA test for differences in calories per cubic meter showed a significant difference between months ($_{ANOVA}$ $F_{2, 103}$ = 11.46; p = 0.001) (Table 4), but no significant difference in diel period ($_{ANOVA}$ $F_{1, 103}$ = 2.79; p = 0.098) or interaction ($_{ANOVA}$ $F_{2, 103}$ = 1.82; p = 0.167) (Table 4; Figure 5). The means for each cell of the 2 x 3 factorial design are shown in Table 5. The total mean for March-April was 164.32 (cal/m^3) and was found to be significantly different from the May mean of 38.78 (cal/m^3) and the February mean of 135.10 (cal/m^3). These mean differences were found using the Tukey's Post-hoc comparison (Table 6).

Zooplankton Caloric Value: Fish Locality vs. Random Sites

A two-way ANOVA showed a significant difference in calories per cubic meter between March-April and May ($_{ANOVA}$ $F_{2, 100}$ = 3.28; p = 0.04) but no significant difference in locality ($_{ANOVA}$ $F_{1, 100}$ = 0.15; p = 0.698) and no interaction ($_{ANOVA}$ $F_{2, 100}$ = 0.36; p = 0.70) (Table 7). Mean calories per cubic meter were slightly higher between fish localities and random sites in February with values of 138.27 and 101.74, respectively, but these differences were not

Table 2. Average calories per gram by composition and month.

Month	Zooplankton Composition	Mean	Std. Deviation	n
February	>= 75% Cladocerans	4727.30	532.40	4
	< 75% Cladocerans	5271.39	213.24	14
	Total	5150.49	372.79	18
March-April	>= 75% Cladocerans	5028.58	403.71	19
	< 75% Cladocerans	4920.58	121.15	2
	Total	5018.29	385.32	21
Total	>= 75% Cladocerans	4976.18	430.85	23
	< 75% Cladocerans	5227.54	233.98	16
	Total	5079.30	380.49	39

Table 3. Two-way ANOVA for calories per gram between zooplankton composition (>= 75% cladocerans and < 75% cladocerans) and months

Source	SS	df	MS	F	Sig.	Partial Eta Squared	Noncent. Parameter	Observed Power[b]
Corrected Model	1111484.78[a]	3	370494.90	2.95	0.046	0.202	8.86	0.65
Intercept	4.55E+08	1	4.55E+08	3629.65	0.00	0.99	3629.66	1
Months	2808.26	1	2808.26	0.02	0.88	0.001	0.022	0.05
Zoo Comp	217579.4	1	217579.40	1.74	0.196	0.047	1.74	0.25
Months * Zoo Comp	486490.8	1	486490.80	3.88	0.057	0.1	3.88	0.48
Error	4389883	35	125425.20					
Total	1.01E+09	39						
Corrected Total	5501368	38						

a. R Squared = .202 (Adjusted R Squared = .134)

b. Computed using alpha = .05

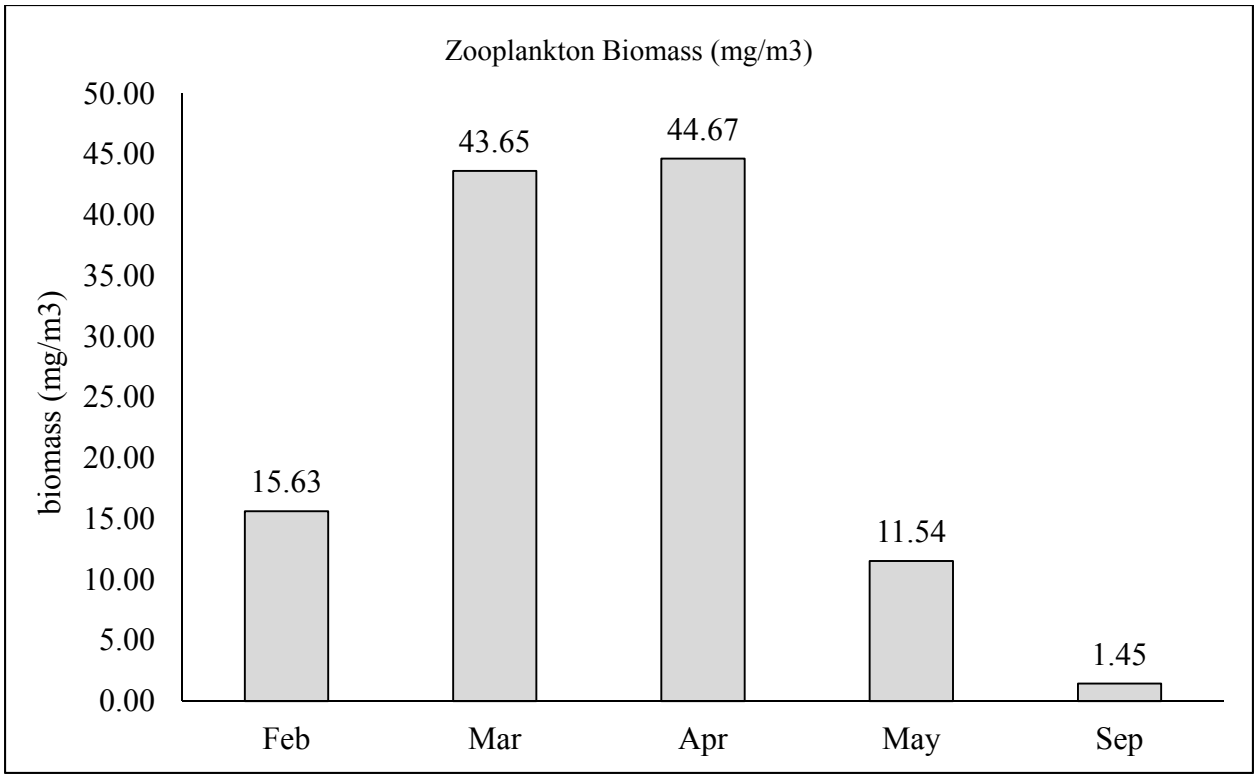

Figure 3. Zooplankton biomass in milligrams per cubic meter across months

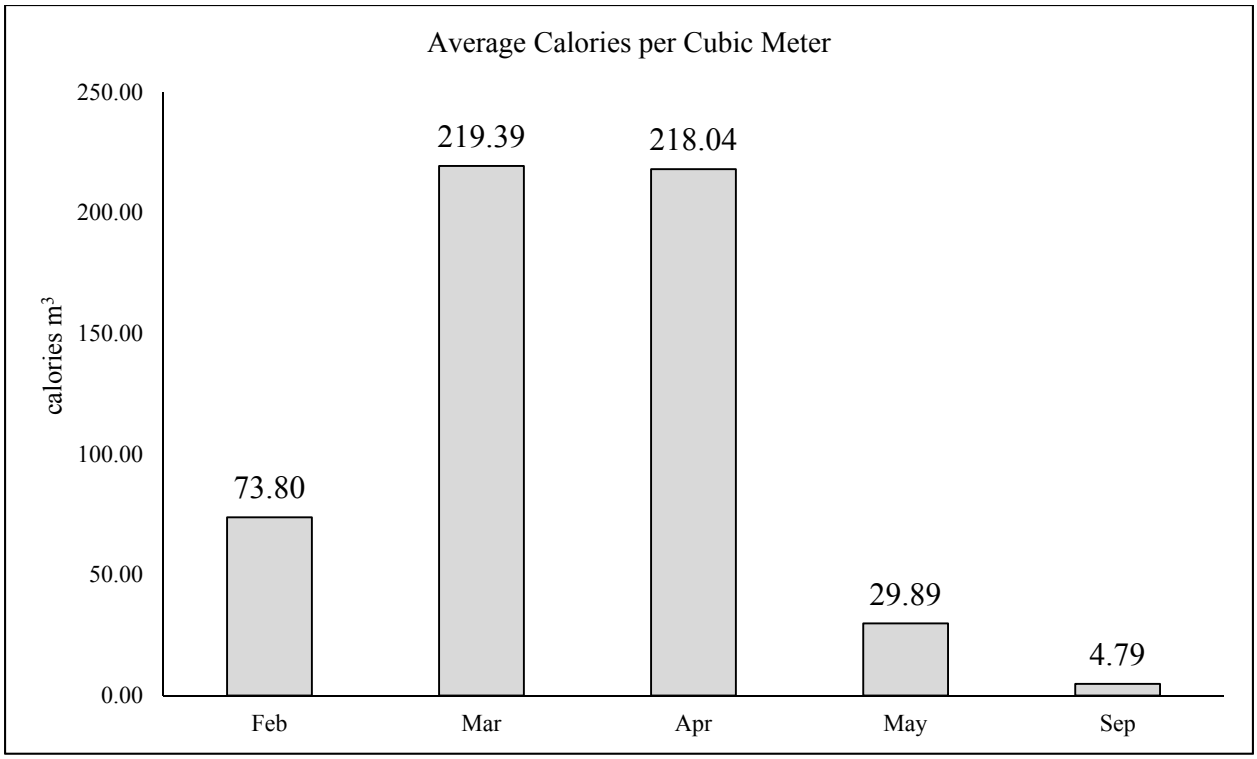

Figure 4. Average calories per cubic meter of zooplankton by month.

Table 4. Two-way ANOVA calories per cubic meter between month and day/night

Source	SS	df	MS	F	Sig.	Observed Power[b]
Corrected Model	8.95[a]	5	1.79	9.90	0.001	1
Intercept	221.90	1	221.90	1226.35	0.001	1
Day/Night	0.505	1	0.51	2.79	0.098	0.38
Month	4.15	2	2.07	11.46	0.001	0.99
Day/Night * Temp	0.66	2	0.33	1.82	0.167	0.37
Error	18.64	103	0.18			
Total	407.63	109				
Corrected Total	27.59	108				

a. R Squared = .324 (Adjusted R Squared = .292)
b. Computed using alpha = .05

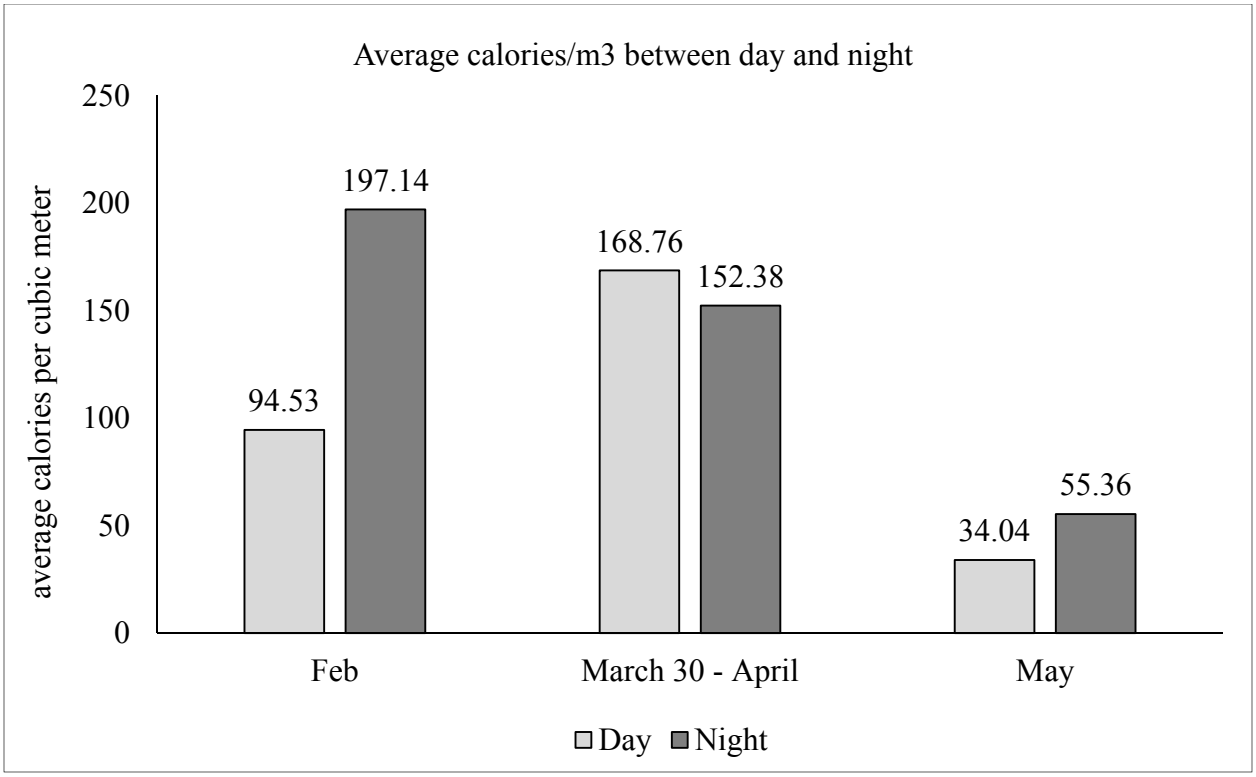

Figure 5. Average calories per cubic meter of zooplankton between day and night

Table 5. Mean calories per cubic meter by month and day versus night

Day / Night	Month	Temperature	Mean	Std. Deviation	n
Day	February	2.49	94.53	86.3	26
	Mar-April	15.31	168.76	130.03	35
	May	21.39	34.04	42.32	14
	Total		117.88	115.52	75
Night	February	2.49	197.14	397.06	17
	Mar-April	15.31	152.38	88.9	13
	May	21.39	55.36	27.18	4
	Total		163.35	285.36	34
Total	February	2.49	135.1	258.98	43
	Mar-April	15.31	164.32	119.59	48
	May	21.39	38.78	39.79	18
	Total		132.06	185.67	109

Table 6. Tukey's post-hoc multiple comparisons between month in day/night comparison

(I) Month	(J) Month	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
February	Mar-April	-.2592*	0.08932	0.012	-0.4716	-0.0468
	May	.5281*	0.11942	0.000	0.2441	0.8121
Mar-April	February	.2592*	0.08932	0.012	0.0468	0.4716
	May	.7873*	0.11757	0.000	0.5078	1.0669
May	February	-.5281*	0.11942	0.000	-0.8121	-0.2441
	Mar-April	-.7873*	0.11757	0.000	-1.0669	-0.5078

Based on observed means.
The error term is Mean Square (Error) = .181.
* The mean difference is significant at the .05 level.

Table 7. Two-way ANOVA for calories per cubic meter between month and locality

Source	SS	df	MS	F	Sig.	Observed Power[b]
Corrected Model	231301.39[a]	5	46260.28	1.36	0.25	0.46
Intercept	910416.10	1	910416.10	26.83	0.00	0.99
Month	222758.60	2	111379.30	3.28	0.04	0.61
Locality	5151.80	1	5151.80	0.15	0.698	0.07
Month * Locality	24177.20	2	12088.60	0.36	0.70	0.11
Error	3393105.16	100	33931.05			
Total	5408232.61	106				
Corrected Total	3624407.55	105				

a. R Squared = .064 (Adjusted R Squared = .017)
b. Computed using alpha = .05

significant (Figure 6). Values increased into March and April: 154.09 and 181.37 cal/m^3 before declining significantly in May: 54.04 and 14.81 cal/m^3. The significant drop in caloric value per cubic meter across season is manifest by differences in zooplankton abundance and not in changes in caloric value per gram zooplankton between sample locations (Table 8). The Tukey's Post-hoc analysis for mean differences is found in Table 9.

4. Discussion

Paddlefish reside in preferred habitats such as impoundments, tail waters, and oxbows characterized by deeper water (≥ 6 m), reduced current (< 5 cm/s), and high zooplankton density (Zigler et al., 2003; Scarnecchia et al., 2009). Such conditions facilitate energy investment into somatic growth and energy reserves such as gonadal fat bodies (Scarnecchia et al., 2007). In a study of 23 oxbow lakes from the lower Mississippi, Miranda et al. (2014) found that lake depth, along with watershed and riparian land use (agriculture) were highly correlated with primary productivity. Conditions in Moon Lake (maximum depth of 12.5 meters and adjacent agriculture) would likely promote primary productivity and trophic diversity. Paddlefish are not selective filter feeders (Smith et al., 2009) and it is assumed that species composition of the water column would be similar to their diet. The zooplankton composition of Moon Lake was 71.25% Cladocerans, 13.78% Cyclopoids, 12.61% Calanoids, and 2.36% other. The zooplankton composition was similar to the zooplankton composition found from stomachs of paddlefish from a stretch of the Big Sunflower River south of Indianola, Mississippi (George et al., 1995). Cladocerans and Copepods were the major representative taxa with Ostracods, Chaoborus, and Chironomids comprising lesser percentages.

Increases in zooplankton body mass associated with cyclomorphosis or optimal grazing, increase their premium as a rich energy source for paddlefish and other zooplanktivores during

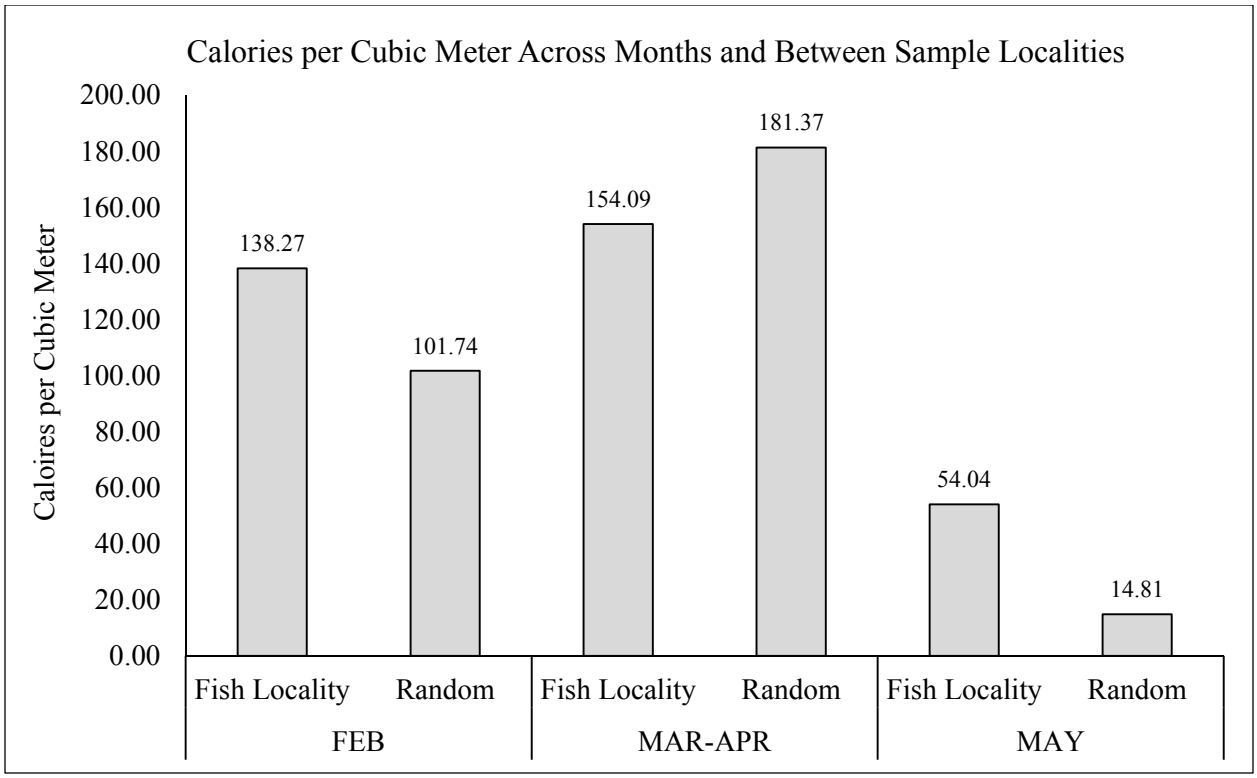

Figure 6. Calories per cubic meter across months and localities

Table 8. Mean calories per cubic meter by month and locality

Month	Locality	Mean	Std. Deviation	n
February	Fish Locality	138.27	301.08	30.00
	Random Locality	101.74	94.38	10.00
	Total	129.14	264.04	40.00
Mar-April	Fish Locality	154.09	109.85	30.00
	Random Locality	181.37	135.88	18.00
	Total	164.32	119.59	48.00
May	Fish Locality	54.04	42.31	11.00
	Random Locality	14.81	20.15	7.00
	Total	38.78	39.79	18.00
Total	Fish Locality	131.90	209.74	71.00
	Random Locality	125.31	126.50	35.00
	Total	129.72	185.79	106.00

Table 9. Tukey's post-hoc multiple comparisons between months

(I) Month	(J) Month	Mean Difference (I-J)	Std. Error	Sig.	95% C.I. Lower Bound	95% C.I. Upper Bound
February	Mar-April	-35.18	39.44	0.646	-129.01	58.64
	May	90.36	52.28	0.200	-34.03	214.74
Mar-April	February	35.18	39.44	0.646	-58.64	129.01
	May	125.54*	50.91	0.040	4.42	246.66
May	February	-90.36	52.28	0.200	-214.74	34.03
	Mar-April	-125.54*	50.91	0.040	-246.66	-4.42

* The mean difference is significant at the .05 level.

favorable conditions. However, the average caloric value per gram of zooplankton did not vary significantly with season or composition in this study. Zooplankton samples taken at locations where fish were present did have slightly higher calories per cubic meter during Feb and May, but showed the opposite trend in March and April (Figure 6). This variation along with a few dense patches skewed the distribution. The differences in densities between these areas were not statistically significant in this study (Table 7). Many factors, including photoperiod, water temperature, water chemistry, food supply, oxygen, competition, and predation, are relevant to the abundance and distribution of zooplankton within lacustrine environments (Beaver and Havens, 1996). Given the lake depth (12.5 meters) and proximity to agriculture, the productivity in Moon Lake is relatively high compared to other North American freshwater lakes (Table 10). The average number of zooplankton per liter in this study was 4.33±2.02 (95% C.I.) organisms. Cladocerans averaged 3.42 ±1.70 (95% C.I.), copepods averaged 0.81±0.39 (95% C.I.), and all others combined averaged 0.105±0.067 (95% C.I.). Moon Lake had both juvenile and adult paddlefish during winter and spring. The high levels of zooplankton may be a reason. The average condition factor of paddlefish in Moon Lake was 2.03±.05 while the average condition factor of paddlefish in Sibley Lake, an oxbow off the Alabama River, was only 1.41±.02. Adult paddlefish were not found in Sibley Lake and may be contributed to lower zooplankton.

It has been suggested in several studies that the advent of rising spring river levels cue paddlefish to move from protected areas; the movements are often concurrent with spawning, cover significant distances, and incur high energy expenditure (Hoxmeier and Devries, 1997; Jennings and Zigler, 2009). However, in this study, these data suggest that decreases in nutrient availability along with decreases in swimming efficiency during warmer months may promote emigration. Two paddlefish in the spring of 2013 moved over 1,448 kilometers from Moon Lake

Table 10. Zooplankton abundance (no. org/liter) in select North American lakes

Country	Lake	Author	*Daphna*	Calanoid	Cyclopoid	*Diaphanosoma*	*Bosmina*	Copepods
USA	Moon Lake	Cage, this study	3.42	0.37	0.44	0.001	0.052	0.81
	Lake Pepin	Burdis and Hoxmeier, 2011	2.1	--	--	--	1.9	15.8
	Lake Okeechobee	Beaver and K. E. Havens, 1996	0.45	10.27	18.05	--	--	--
Canada	Big Salmon		1.1	1.21	1.39	0.21	0.09	--
	Little Salmon		7.47	3.17	0.51	0.55	0	--
	Little Caesar		3.26	15.56	2.89	1.4	0	--
	Arab		8.99	0.11	2.73	0	0	--
	Doe		0.39	0.28	0.1	0	0	--
	South Otter		0.39	0.07	0.64	0	0	--
	Labelle		3.21	7.04	6.09	0.87	0.6	--
	Upper Rock		0.05	0.21	0.03	0	0	--
	Warner		1.28	0.51	18.53	1.28	0	--
	Elbow		2.48	0.95	8.15	0.31	0.1	--
	Lindsay	Khrysta Lyn and Danielle Carter, 2014	0.84	1.95	6.71	0	0.27	--
	Pool		0.65	1.41	11.08	0.54	0.43	--
	Round		0.12	1.29	0.45	0.08	0	--
	Long		0.27	0.12	0.32	0.02	0	--
	Whitefish		0	1.63	18.75	45.66	0.82	--
	Sand		0.06	0	4.08	1.3	2.74	--
	Cranberry		5.16	8.97	8.42	0	5.16	--
	Colonel Bay		1.47	2.61	0.98	0	1.79	--
	Collins		0.95	0.06	3.89	0.55	4.3	--
	Loughborough		9.75	5.66	8.89	0.46	0.19	--

into the Missouri River. The migration to the Mississippi River alone was 506.9 kilometers. Whether arrival to Moon Lake is fortuitous or not, the seasonal residence in favorable habitat, such as Moon Lake, promotes preparedness for an arduous seasonal migration. Such distances are often characterized by high energetic expenditure. The remote geography of Moon Lake suggests that it may be a deliberate seasonal destination for paddlefish in preparation for migration.

5. Conclusions

With the ability of paddlefish to exploit nutrient rich areas of zooplankton, it was predicted that samples taken from sites where paddlefish were located would have a higher zooplankton density and/or caloric value than areas sampled at random. However, no significant differences in zooplankton density or caloric value were found between sites. Generally, zooplankton concentrations were slightly higher in areas of fish presence, but the productivity of the lake as a whole is so high, during some months, that paddlefish energetic needs are met without extensive searching.

It is assumed that increases in zooplankton productivity will provide energetic benefits to paddlefish. Productivity is a function of both baseline caloric values as well as zooplankton abundance: the product of which will be the total caloric availability at any given period. In this study, the number of calories per gram zooplankton did not vary, therefore, zooplankton abundance was the primary determinant of energy availability. Zooplankton abundance measured in density per cubic centimeters, increased significantly during April and May. The composition of zooplankton consisted of equivalent percentages of Cladocerans and Copepods during cooler months, but showed a progressive shift to mostly Cladocerans by May. The total

calories per tow did not vary significantly with changes in composition. Zooplankton abundance showed significant reduction by September coinciding with fish movements from the lake.

CHAPTER III

SEASONAL CHANGES IN SWIMMING PERFORMANCE IN THE AMERICAN PADDLEFISH, POLYODON SPATHULA: MEASURES OF METABOLIC RATE

1. Introduction

Locomotion is influenced by morphological, biochemical, and physiological traits that provide the "operational framework" by which an organism balances the energetic costs of performance with the metabolic demands of activity under ambient environmental conditions and available prey (Huey, 1991; Claireaux and Lefrançois, 2007). Physiologists have grouped swimming into three categories (sustained, prolonged, and burst) according to the duration, intensity, and basic energy-yielding pathway supporting each level (Webb, 1975). Sustained swimming speeds (> 200 minutes) are used for activities of routine behaviors such as station holding, foraging, exploration, and territorial defense and are supported in many species by the thin strip of lateral, slow, oxidative (SO) red muscle fibers extending the length of the lateral line (Webb, 1975; Jobling, 1995). Recruitment of intermediate fast oxidative glycolytic (FOG) pink fibers involve glycolytic adenosine triphosphate (ATP) production and can result in bouts of increased swimming limited by the production of lactic acid. Durations of prolonged swimming are defined as lasting greater than 20 seconds but shorter than 200 minutes. The bulk of muscle fibers in fish are fast glycolytic (FG) fibers which support the short bursts lasting less than 20 seconds and are strictly supported by phosphocreatine stores and glycolysis (Jobling, 1995).

Of all the variables that may affect swimming performance, (oxygen tension, photoperiod, water depth, temperature, level of activity, turbidity, and gas/nutrient transport and

exchange) temperature has the most demonstrable effect. Temperature affects the rate of metabolic reactions, as well as, dissolved oxygen concentrations in aquatic systems (Diana, 1995; Jobling, 1995). As ectotherms with limited insulation and high conductive heat loss, most fish rapidly conform to ambient temperature changes (Schmidt-Nielsen, 1990). Many researchers (Winberg, 1956; Fry, 1971; Brett, 1964; Schmidt-Nielsen, 1972; Brett and Groves, 1979; Penczak, 1990) have emphasized the importance of temperature on swimming performance and its relevance to studies of bioenergetics and aquatic locomotion (Hartman and Hayward, 2007).

Ram ventilation is a swimming behavior that produces sufficient pressure during forward movement with the mouth agape to perfuse water over the gills (Graham, 1990). The advantage is conspicuous; a large number of fishes switch the mechanism of gill ventilation from opercular pumping to ram ventilation at higher swimming speeds (Burggren and Bemis, 1992; Sims, 1999). The switch from using opercular to trunk musculature is associated with a reduction in cost without a decrease in swimming speed and increases the energy efficiency at maximum cruising speeds. In some species, like bluefish and striped bass, energetic savings may be as high as 50 percent (Freadman, 1981). Although the benefits of switching to ram ventilation among taxa are universal, the energetic savings is species dependent, and will fluctuate with environmental conditions and ration (Roberts, 1975; Freadman, 1979; Kitchell, 1983).

Environmental perturbations such as hypoxia can often reduce the swimming efficiency of ram ventilators. Carlson and Parsons (1998) noted that ram ventilating bonnethead sharks, *Sphyrna tiburo*, increased their average swimming speed from 24 to 40 cm/s and oxygen consumption rate from 115 to 350 mg O_2 kg^{-1} h^{-1} as oxygen concentration decreased from 6 to 3 mg l^{-1}. This was over a three-fold increase in the total metabolic rate with the onset of hypoxia.

Of the subset of ram ventilators, the paddlefish, *Polyodon spathula*, and the basking shark, *Cetorhinus maximus*, are the only two obligate, ram ventilating, filter feeders (Burggren and Bemis, 1992; Sims, 1999). Larger sharks such as the whale shark, *Rhincodon typus*, and megamouth shark, *Megachasma pelagios*, filter zooplankton through a repetitive action of suction and swallowing, as opposed to continuous filtering with the mouth agape (Diamond, 1985; Compagno, 1990). As obligate ram ventilating filter feeders, paddlefish and basking sharks are subject to increased drag due to bouts of swimming with their mouth agape. Such drag increases energy expenditure and can be 75% higher than routine cruising speeds (Burggren and Bemis, 1992; Sims, 1999) . Sims reported an inverse relationship in swimming speed of the basking shark and the prey per unit volume in the water column. As the density of prey items increased, swimming speed was reduced as much as 24% (Sims, 2000).

Paddlefish have little ability for station holding in reduced currents or swimming at slow speeds. In controlled settings, observations of ventilation frequencies were as low as 50 to 80 gill beats per minute before switching to ram ventilation at speeds as low as 5.7 cm s^{-1} at 24°C under normoxic conditions (Burggren and Bemis, 1992). Paddlefish have a low capacity for anaerobic metabolism and quickly succumb to environmental hypoxia around 89 mm Hg at 25-26°C (Singer and Ballantyne, 2004; Aboagye and Allen, 2014). However, lower temperature (16°C) tends to extend the ability of paddlefish to tolerate oxygen partial pressures as low as 74 mm Hg (Aboagye and Allen, 2014). Dong (2009) reported paddlefish weighing around 15 grams had an asphyxiation point between 3.069 to 3.40 mg/l at 19-20°C and 27-28°C, respectively. Aboagye and Allen (2014) reported that paddlefish required a dissolved oxygen concentration >4.7 mg/l to support basal aerobic metabolism between temperatures of 18 and 26°C.

Understanding swimming efficiency and its relationship to prevalent biotic and abiotic energetic functions is the logical first step in answering questions about energy allocation and behavioral activity during periods of energetic stress and compensation. The swimming speed with the lowest energetic cost of transport, U_{opt}, is often at intermediate cruising speeds and may be used in search of prey or suitable habitat (Jobling, 1995). Even at low speeds and low energy expenditure, the inability to find and consume adequate amounts of prey may cause reduced growth, starvation, or even death (Videler, 1993; Hartman and Hayward, 2007).

The critical foraging threshold for paddlefish is presently unknown. Conditions, both biotic and abiotic, influence the amount of prey intake necessary to support metabolism within a given environment. These oxbows with little current and plentiful prey may provide sufficient energy for growth and reproduction during profitable periods, but the increase in energetic cost of transport during warmer months along with a decrease in environmental dissolved oxygen concentrations may cause a critical period for paddlefish (Fry, 1971; Claireaux and Lefrançois, 2007).

Most allocation to growth is seasonal and dependent on food availability and local environmental conditions (Jennings and Zigler, 2009). Growth of Age-1 paddlefish differed by as much as 310 mm eye-to-fork-length (EFL) between populations in Lewis and Clark Reservoir on the North Dakota/Nebraska border and populations from Fort Gibson Reservoir in Oklahoma. Age-1 paddlefish in Louisiana were intermediate between the two populations ranging from 411 to 455 mm EFL (Houser and Bross, 1959; Ruelle and Hudson, 1977; Reed et al. 1992). Somatic growth occurs rapidly in the first five years of paddlefish life with an initial investment into the development of gonadal fat bodies (GFB) (Scarnecchia et al., 2007). The rate of deposition and use of GFB's during early reproductive years may play a crucial role in the periodicity and

length of pre-spawning migrations (Scarnecchia et al., 2007). Delay in age of maturity between female and male cohorts differ by as much a four years in southern populations and up to nine years in northern populations. This disparity in reproductive maturation between the sexes and the variability of development of somatic growth and gonadal fat bodies in early development may segregate the use of backwater sanctuaries and oxbow lakes based on maturity and life stage. It is of interest to determine if paddlefish's investment in locomotion increases during periods of abundant food availability or becomes more conservative.

The objectives of this study were to: 1) determine the effect of swimming speed on metabolic rate across season, 2) determine how the cost of transport (mg O_2 hr^{-1}) changes with swimming speed across season, and 3) compare feeding optimality across seasons through a cost-to-benefit analysis. The cost-of-benefit analysis will draw from results from both chapter two and chapter three and chapters will be reference as needed.

2. Materials and Methods

Fish Collection and Transport

Fish were collected using a 100 x 2.43 meter floating gill net from Moon Lake in Coahoma County, in northwest Mississippi from November of 2013 through September of 2014. Gill nets were checked every 0.5 hours to minimize fish stress and time of entanglement. Paddlefish ranged in size from 780 - 1280 mm eye-to-fork length (2.6 to 4.2 feet EFL), and only healthy individuals were used. Fish liberated from nets were placed into a six foot live well and motored to Moon Lake Landing boat launch. Fish were transported from the boat launch to a respirometer (described below) by gurney or truck. The average transport time from capture to the tank was 16 minutes.

Portable flow tunnel respirometer

A large portable Brett-type swim tunnel made of stainless steel piping (44 cm diameter) and a rectangular Plexiglas working section measuring 243.84 x 91.44 x 91.44 centimeters was used to conduct swimming tests (Figure 7). The tunnel was set up at the Moon Lake Landing Pavilion roughly 60 meters from the boat launch. The total working volume of the tunnel was 2917 liters. Water flow was generated with a motorized impeller capable of generating water speeds between 53.91 and 167.39 centimeters per second within the working section of the swim tunnel. A tarp was draped over the working section of the tunnel to reduce fish stress. Two rectangular baffles were installed forward and aft of the working section to promote rectilinear flow. An YSI 556 hand-held multiple parameter meter was used to simultaneously measure dissolved oxygen, pH, conductivity, and temperature.

The tank was filled, on site, using dechlorinated tap water and diffused with pure oxygen using a pressurized oxygen tank until the dissolved oxygen levels reached no less than 7.5 milligrams per liter within the swim chamber prior to the addition of a fish. A blank control test, in the absence of fish, was run to check the baseline rate of oxygen depletion from the respirometer system to calculate a correction factor.

Swimming Protocol

Fish were placed into the working section of the respirometer and allowed a one-hour acclimation period before initial swimming trials, during which tunnel velocity was maintained at a minimal speed of 54 centimeters per second. Following the acclimation period the swimming chamber was topped with water, sealed and latched with the lid, and vacated of trapped air through a release valve.

Figure 7. US Army Engineer Research and Development Center tunnel respirometer

Following acclimation, fish were subjected to successive one-hour swimming bouts at currents of 76.05, 91.27, 106.50, and 121.72 centimeters per second. Fish continued to swim in this pattern until they were no longer able to maintain position in the water column and became impinged on the posterior wall of the working section. Estimates of metabolic rates were calculated using the following computation: $VO_2 = b \times v$, where, VO_2 is the milligrams of oxygen consumed per hour, b is the rate of oxygen decline within the chamber, and v is the total volume of water. Metabolic rates per fish biomass were reported as mg O_2 kg^{-1} h^{-1}.

Tail beat frequency and ventilation rates were recorded every other minute during each swimming bout. Tail beat frequency was defined as the number of complete lateral side-to-side movements of the caudal fin, and ventilation rate was defined as the number of times the fish visibly opened and closed its mouth to ventilate the gills. All swimming trials were videotaped to verify tail beat counts and ventilation rates.

Following swimming trials, eye to fork length (EFL), mouth width (MW), mouth height (MH), and rostral length (RL) were measured to the nearest millimeter. Weight was measured with a Chatillon ® hanging scale to the nearest kilogram before releasing the fish back into Moon Lake.

The increase in metabolic rate of paddlefish with an increase in 10°C (Q_{10}) was measured with the following equation: $Q_{10} = (K_2/K_1)$ ^ $(10/T_2\text{-}T_1)$ where T_2 and T_1 were the average temperatures during May and January, respectively. Q_{10} was calculated for each of four swim speeds tested by replacing K_2 and K_1 with the appropriate weight-specific metabolic measured during May and January, respectively (Table 11).

Table 11. Metabolic rates and temperatures used to calculate Q_{10}

swim speed cm/s	metabolic rate (mg O_2 kg^{-1} h^{-1})		Temperature (°C)	
	January	May	January	May
76.05	90.78	152.02	10.34	24.30
91.27	66.37	205.99	10.34	24.30
106.5	56.09	106.44	10.34	24.30
121.72	61.95	103.89	10.34	24.30

Calculating Cost-to-Benefit Ratio

Mouth width (MW) and mouth height (MH) were used to calculate filtration volumes of paddlefish swimming at five swim speeds (53.00, 76.05, 91.27, 106.50, and 121.72 cm/s) in order to analyze changes in cost-to-benefit ratios across season. The calories obtained while suspension feeding (measured in total calories) are considered here as the energetic benefits in the cost-to-benefit ratio. Tow samples of zooplankton were taken (see chapter two). The volume of water sampled during a tow event was calculated by the following equation (Figure 8): π x (net diameter) ^{2} x distance of tow sample / 4. The estimate of zooplankton density/abundance (organisms/m^3) were calculated by dividing the total number of organisms by the volume sampled. The caloric concentration (calories/m^3) of zooplankton samples were estimated by dividing the total number of calories in the zooplankton sample (measured using a Parr 1266 oxygen bomb calorimeter – chapter two) by the total volume sampled. The caloric concentration estimates calculated from zooplankton samples at a given season were used to calculate the total number of calories a paddlefish could theoretically filter from the water column while suspension feeding at a given speed at a given season (cm/s) by multiplying the average estimate of the caloric concentration of zooplankton (cal/m^3) from tow samples by the total volume of water (m^3) filtered by a paddlefish (m^3). This value represents the benefits (in calories) in the cost-to-benefit ratio. The estimate of the volume of water that a paddlefish could filter (m^3) was calculated by the following: π x [(0.25 x MH x MW) $^{0.5}$ x 2] ^{2} x distance / 4, where (MW) equals mouth width in centimeters and (MH) equals mouth height in centimeters (Figure 8). The distance is directly proportional to swim speed as measured in centimeters per second. Swim speed (cm/s) was converted to centimeters per hour to obtain distance (cm/h). The final product was divided by 100,000 to convert to cubic meters. The costs (total calories/hour) in the

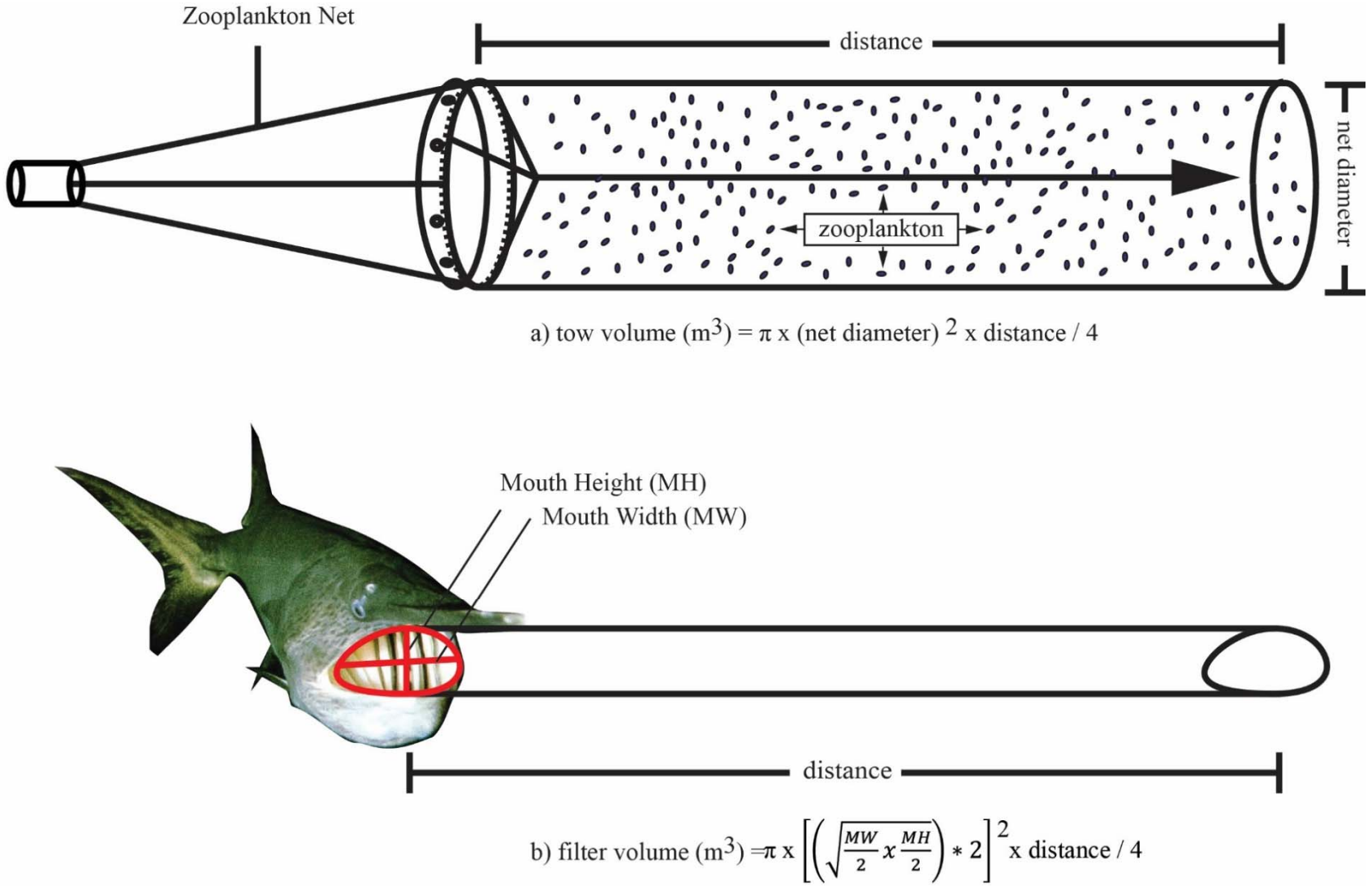

Figure 8. Methods for estimating the tow volume of zooplankton samples (m^3) and the filter volume of paddlefish (m^3).

cost-to-benefit ratio were calculated by the following formula: fish mass (kg) x weight-specific metabolic rate at given swim speed (mg O_2 kg^{-1}) x oxycalorific coefficient for fish (3.25 cal g^{-1}) (Brafield and Solomon, 1972). The product is the number of calories expended by a paddlefish over one hour swimming at the tested swim speed.

Statistical Analysis

Kruskal-Wallis one-way ANOVA of ranks were used to test for: 1) significant differences between weight-specific metabolic rates at each of four separate swimming speeds (76.05, 91.27, 106.50, and 121.72 cm/s), and 2) significant differences between the cost of transport (COT) at each of four separate swimming speeds (76.05, 91.27, 106.50, 121.72 cm/s). No significant differences were found between weight-specific metabolic rates at any swim speed or between the COT at any swim speed.

3. Results

Thirty-three fish were swum between November of 2013 and September of 2014. Seven of the 33 fish were non-performers. Non-performers were defined as fish that did not acclimate or successfully complete a single bout at any given swimming speed. From the twenty-six fish that were successfully swum during the study, the total number of swimming speeds for which oxygen consumption data were collected is given in Table 12. Oxygen consumption rates were not recorded during acclimation periods. The average absolute metabolic rate (mg O_2 h^{-1}) (Table 13) and weight-specific metabolic rate (mg O_2 kg^{-1} h^{-1}) (Table 14) were calculated for each swimming speed per month and plotted in Figure 9 and Figure 10.

The weight specific metabolic rates (mg O_2 kg^{-1} h^{-1}) were converted to cost of transport by converting mg O_2 to calories by multiplying by the oxycalorific coefficient of 3.25 calories per mg O_2 (Brafield and Solomon, 1972). The product of the calories per kilogram fish mass per

Table 12. Total number of swimming bouts per swimming speed for each field stint.

Date	Fish ID	Swimming Speed cm sec^{-1}								
		26	54*	59	61	76	91	107	122	137
11/14/2013	SWFALL004		◦		•	•	•			
11/14/2013	SWFALL005		◦		•	•				
1/13/2014	SWWIN006		•			•	•	•	•	
1/14/2014	SWWIN007		◦			•	•	•		
1/14/2014	SWWIN008		•	•		•	•	•	•	
1/15/2014	SWWIN009		◦			•	•	•	•	
1/16/2014	SWWIN010		◦			•	•	•	•	
1/16/2014	SWWIN012		◦				•	•	•	•
2/24/2014	SWWIN025		◦	•		•	•	•		
2/24/2014	SWWIN026		◦	•		•				
2/25/2014	SWWIN028		•			•	•	•	•	
2/25/2014	SWWIN029		•							
2/26/2014	SWWIN032	•	•			•	•	•		
2/26/2014	SWWIN033	•	•			•	•			
2/27/2014	SWWIN034		•			•	•	•	•	
2/27/2014	SWWIN035		•			•	•	•		
5/19/2014	SWSPRG046		•			•	•	•	•	•
5/20/2014	SWSPRG047		•			•	•	•	•	
5/21/2104	SWSPRG048		•			•				
5/21/2104	SWSPRG049		•			•	•			
5/22/2104	SWSPRG050		•			•	•	•	•	•
9/09/2014	SWFALL051		◦			•	•	•	•	•
9/10/2014	SWFALL054		•			•	•			
9/11/2014	SWFALL055		•			•	•	•	•	
9/11/2014	SWFALL057		◦			•	•			
9/11/2014	SWFALL058		◦			•				

∗ denotes acclimation speed; ◦ oxygen consumption not recorded during acclimation.

Table 13. Average absolute oxygen consumption rates (mg O_2 h^{-1}) per swim speed and month.

	swim speed (cm/s) →	76.05	91.27	106.5	121.72
	swim speed (km/h) →	2.74	3.29	3.83	4.38
Month	November 2013	1526.80	983.27	--	--
	January 2014	2316.02	1744.43	1485.46	1559.59
	February 2014	1566.70	1410.02	1746.53	2289.57
	May 2014	2422.91	2952.01	2401.66	2308.32
	September 2014	2520.28	2432.77	2660.31	2572.80

Table 14. Average weight-specific oxygen consumption rates (mg O_2 kg^{-1} h^{-1}) per swim speed and month.

	swim speed (cm/s) →	76.05	91.27	106.50	121.72
	swim speed (km/h) →	2.74	3.29	3.83	4.38
Month	November 2013	71.43	50.42	--	--
	January 2014	90.78	66.37	56.09	61.95
	February 2014	100.21	99.22	87.65	105.91
	May 2014	152.02	100.73	106.44	103.89
	September 2014	92.63	90.63	86.17	103.61

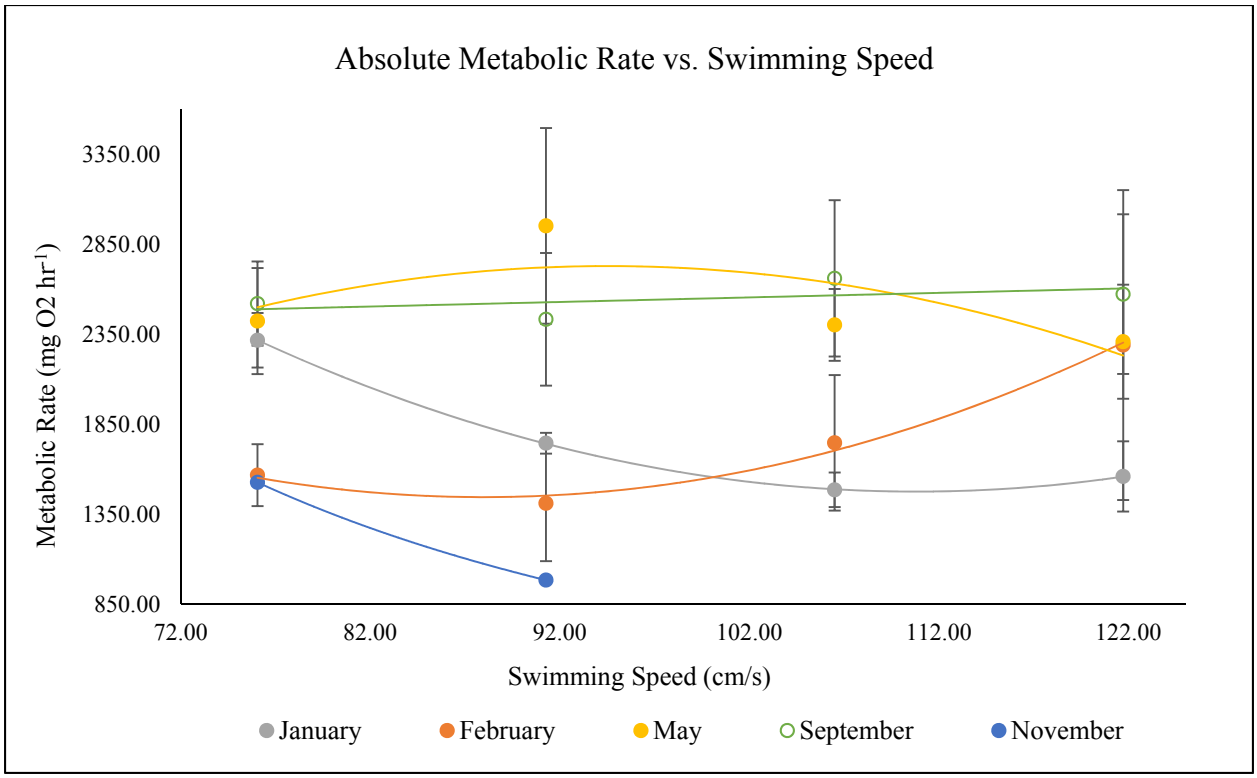

Figure 9. The relationship between absolute metabolic rate and swimming performance (±S.E.). Equations: January ($y = 0.6966x^2 - 154.38x + 10029$); February ($y = 0.7549x^2 - 132.84x + 7289$); May ($y = -0.6715x^2 + 126.93x - 3269.6$); September ($y = -2E\text{-}06x^2 + 2.5303x + 2296.3$); November ($y = 5E+07x^{-2.412}$).

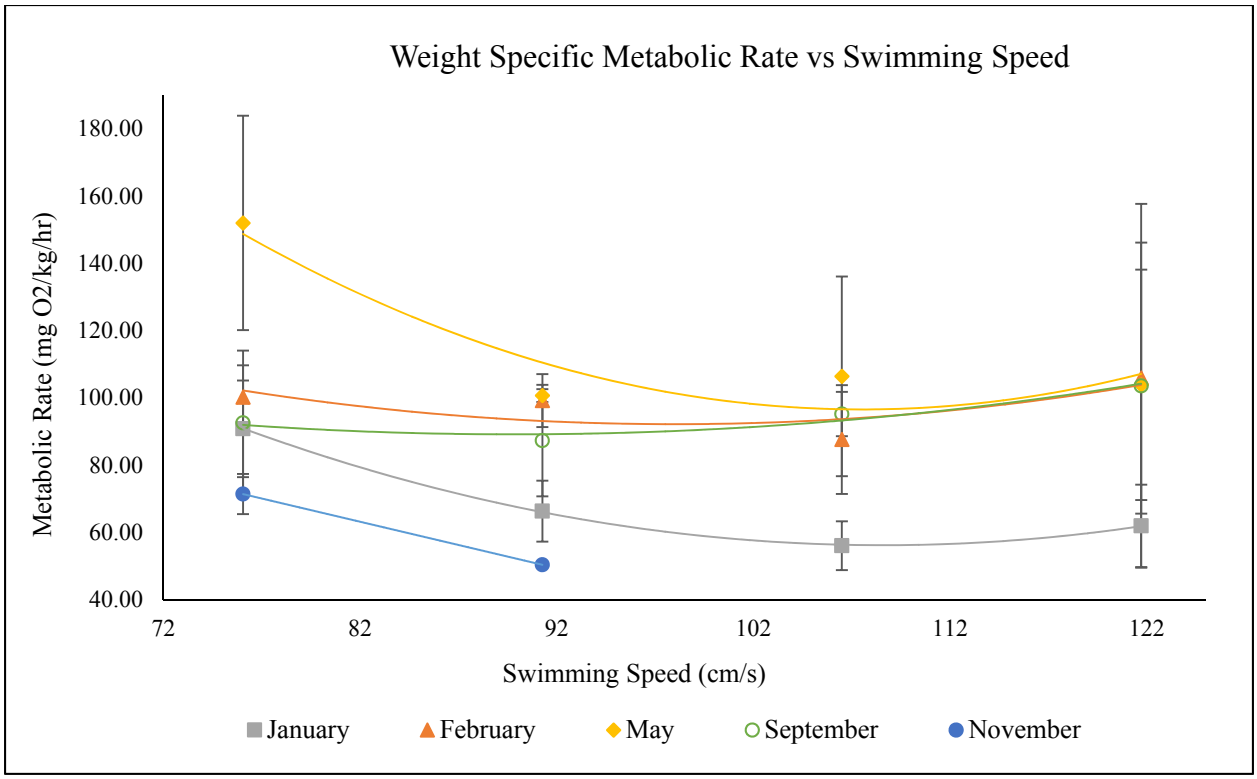

Figure 10. Relationship of metabolic rate and swimming performance (± S.E.). Equations: January ($y = 0.0328x^2 - 7.1131x + 442.46$); February ($y = 0.0208x^2 - 4.0699x + 291.66$); May ($y = 0.0526x^2 - 11.312x + 704.86$); September ($y = 0.0148x^2 - 2.6564x + 208.48$); November ($y = -1.3803x + 176.4$).

hour was divided by the distance, in kilometers, a paddlefish would travel over one hour swimming at each of the four swimming speeds tested (76.05, 91.27, 106.50, and 121.72 cm/s). The products of calories per kilogram fish mass per kilometer were divided by 1,000 to produce the cost of transport as the calories expended to move one gram of body mass one kilometer (COT) (Table 15). The relationship of the COT to fish mass in kilograms was plotted in Figure 11.

The average cost of transport for each swimming speed tested (76.05, 91.27, 106.50, and 121.72 cm/s) were graphed for each month (Figure 12). Four Kruskal-Wallis one-way ANOVA of ranks were used to test for significant differences between COT and swim speed (76.05, 91.27, 106.50, and 121.72 cm/s). No significant differences were found between the COT at any of the four swimming speeds tested.

The COT was highest in May (0.1805 cal/g/km) at a swimming speed of 76.05 cm/s and lowest in January (0.046 cal/g/km) at swimming speeds 121.72 cm/s (Figure 12). The COT at 76.05 cm/s was lowest in November (0.0848 cal/g/km) and highest in May (0.1805 cal/g/km). The COT during January, February, and September ranged between 0.1078 and 0.1190 calories per gram per kilometer, respectively. At swimming speeds of 91.27 cm/s the COT was highest in May (0.0996 cal/g/km) and lowest during November (0.0499 ca/g/km). The COT ranged from 0.0656 to 0.0981 cal/g/km from January to February and was 0.0864 cal/g/km in September. The COT at the highest swimming speed (121.72 cm/s) was similar during February, May, and September at 0.0785, 0.0771, and 0.0768 cal/g/km, respectively. The COT during January was 0.046 cal/g/km. This was nearly a 60% reduction in the COT during January compared to the other months at the highest swimming speed tested.

Table 15. Conversion table of weight-specific metabolic rate (mg O_2 kg^{-1} h^{-1}) to cost of transport (cal g^{-1} km^{-1})

Month	Temp °C	cm s^{-1}	mg O kg^{-1} h^{-1}	cal kg^{-1} h^{-1}	distance h^{-1} (km)	cal kg^{-1} km^{-1}	cal g^{-1} km^{-1}
Jan	10.48	76.05	90.78	295.04	2.74	107.77	0.1078
Jan	10.36	91.27	66.37	215.71	3.29	65.65	0.0656
Jan	10.41	106.50	56.09	182.30	3.83	47.55	0.0475
Jan	10.52	121.72	61.95	201.34	4.38	45.95	0.0459
Feb	9.42	76.05	100.21	325.67	2.74	118.95	0.1190
Feb	9.35	91.27	99.22	322.45	3.29	98.13	0.0981
Feb	10.05	106.50	87.65	284.87	3.83	74.30	0.0743
Feb	11.55	121.72	105.91	344.20	4.38	78.55	0.0785
May	23.64	76.05	152.02	494.06	2.74	180.46	0.1805
May	23.05	91.27	100.73	327.36	3.29	99.63	0.0996
May	23.99	106.50	106.44	345.92	3.83	90.23	0.0902
May	24.16	121.72	103.89	337.66	4.38	77.05	0.0771
Sept	27.12	76.05	92.63	301.05	2.74	109.96	0.1100
Sept	27.20	91.27	87.31	283.76	3.29	86.36	0.0864
Sept	26.74	106.50	95.22	309.47	3.83	80.72	0.0807
Sept	26.88	121.72	103.61	336.73	4.38	76.84	0.0768
Nov	15.43	76.05	71.43	232.15	2.74	84.79	0.0848
Nov	15.79	91.27	50.42	163.88	3.29	49.87	0.0499

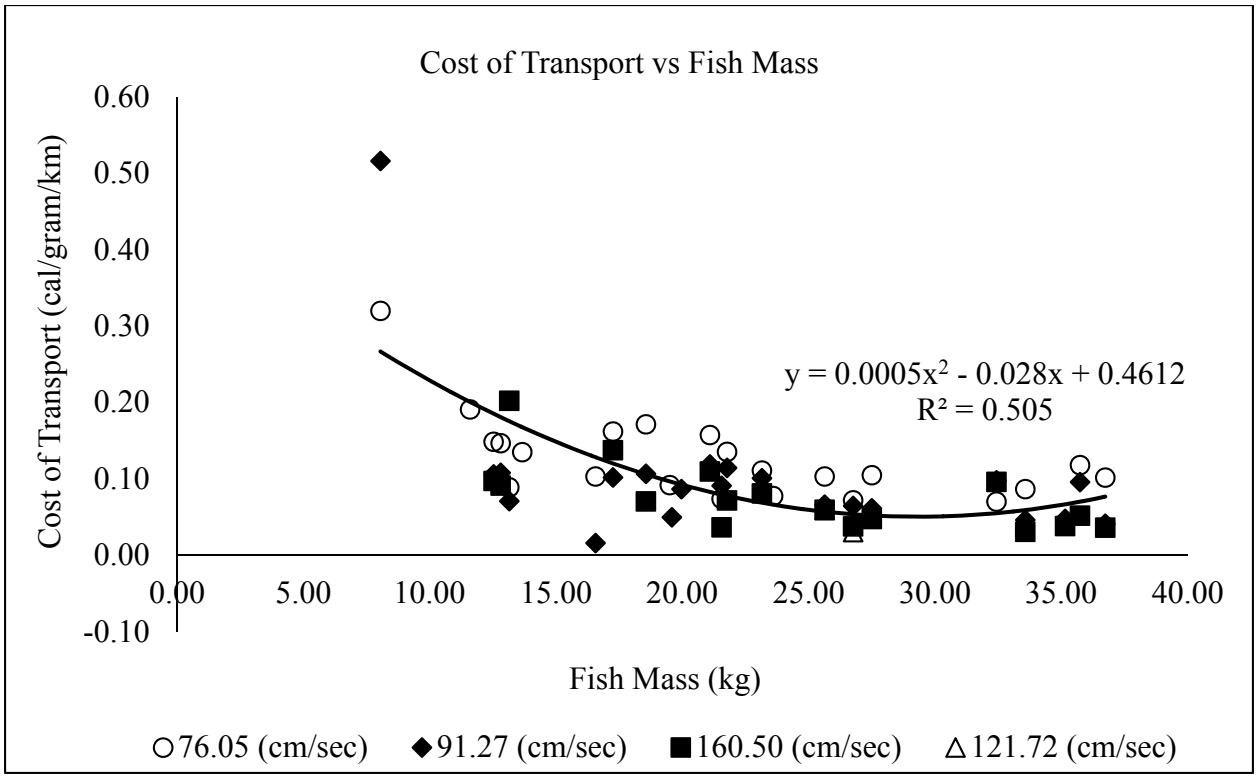

Figure 11. Cost of transport versus fish mass

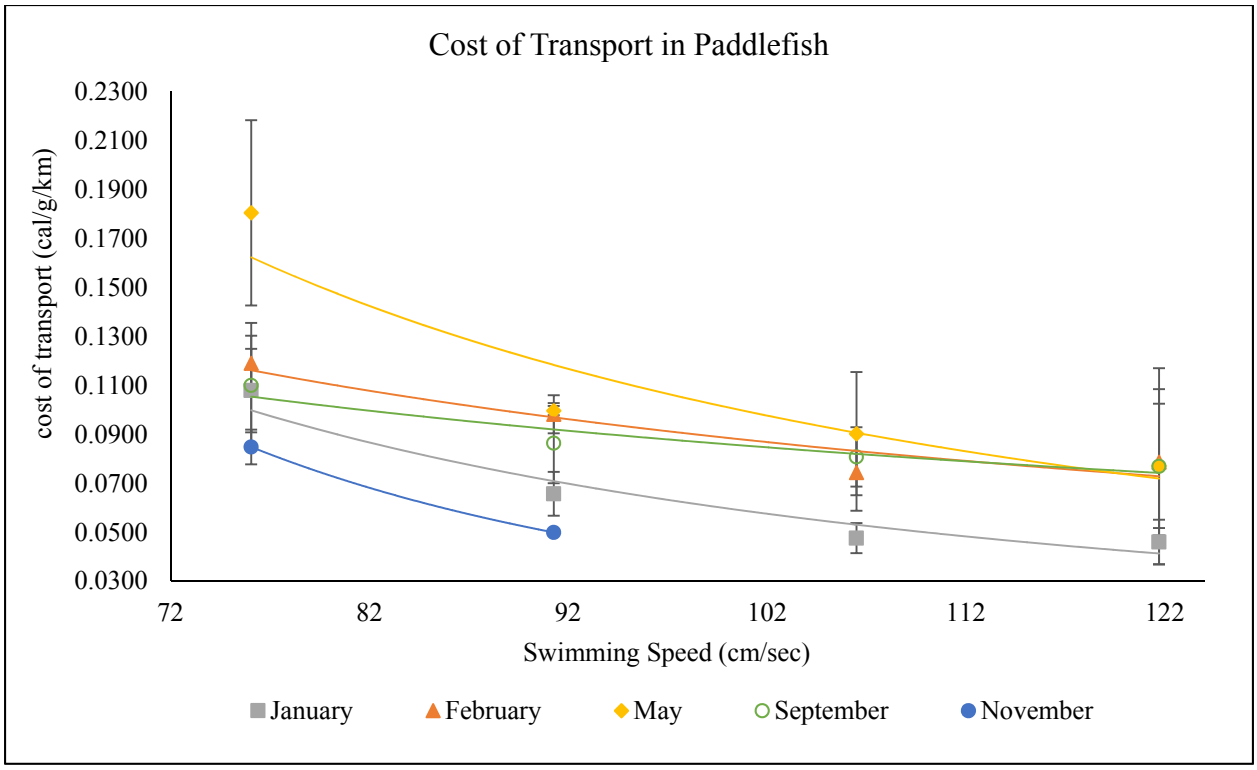

Figure 12. The cost of transport across swimming speeds and months for paddlefish (±S.E.). Equations: January ($R^2 = 0.9245$; $y = 337.48x^{-1.876}$); February ($R^2 = 0.8637$; $y = 8.5116x^{-0.992}$); May ($R^2 = 0.8897$; $y = 292.38x^{-1.731}$); September ($R^2 = 0.9044$; $y = 2.6639x^{-0.746}$); November ($R^2 = 1$; $y = 25147x^{-2.909}$).

Tailbeat frequency and ventilation rate were recorded during swimming trials and presented as the number of tailbeats per minute at four swim speeds (76.05, 91.27, 106.50, 121.72 cm/s). Paddlefish eye-to-fork length (cm) was divided by tunnel speed (cm/s) to calculate the relative swimming speed of paddlefish in body lengths per second (BLS). Tailbeat frequency and BLS were significantly correlated (Spearman's rho) at swimming speeds of 76.05 and 91.27 cm/s with correlation coefficients of 0.624 and 0.457, respectively. The linear regression of tailbeat frequency and BLS calculated at tunnel speeds of 76.05 cm/s ($F_{1, 20} = 15.845$, $p = .001$, $\alpha = 0.05$) and 91.27 cm/s ($F_{1, 17} = 10.676$, $p = .005$, $\alpha = 0.05$) were both significant (Figure 13; Figure 14). No significant correlation was found between tailbeat frequency and BLS at swimming speeds of 106.50 or 121.72 cm/s (Figure 15 and Figure 16). Average tailbeats were much lower at higher speeds than at slower speeds and were considerably higher at slower speeds during February and May (Table 16), but no significant difference across distributions were found using a nonparametric independent samples Kruskal-Wallis one-way ANOVA ($\chi^2 = 5.951$, $p = 0.114$, $\alpha = 0.05$). At the swim speeds tested in this study, smaller fish (i.e., fish with higher BLS at swim speed) had higher tailbeat frequencies than larger fish (i.e., fish with lower BLS at swim speed) (Figure 13 and Figure 14). No significant correlation was found between ventilation rate (#/min) and swimming speed measured as body lengths per second at speeds of 76.05 cm/s ($\rho = 0.078$, $p = 0.751$) or 91.27 cm/s ($\rho = -0.102$, $p = 0.651$) using a Spearman nonparametric bivariate correlation (Figure 17 and Figure 18). Correlation between ventilation rate (#/min) and swimming speed at 106.60 and 121.72 cm/s were not calculated.

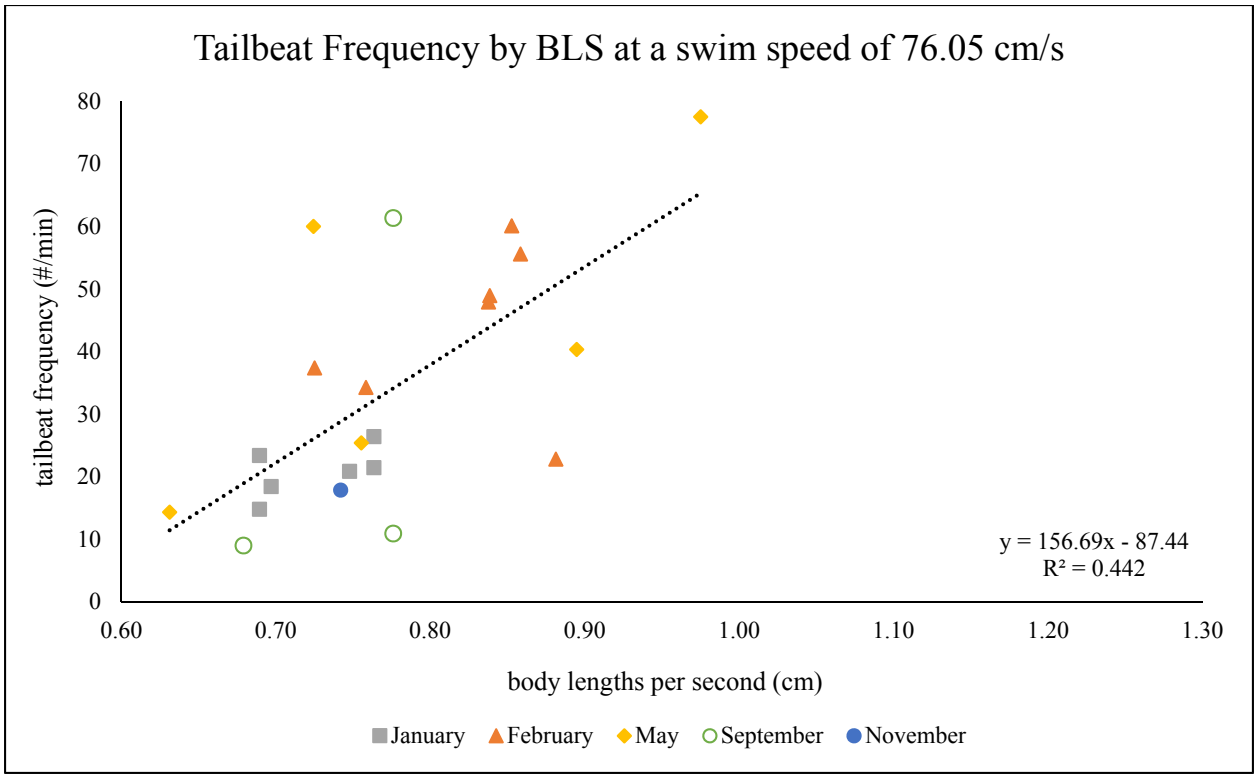

Figure 13. Relationship between tailbeat frequency and body lengths per second at a swimming speed of 76.05 cm/s

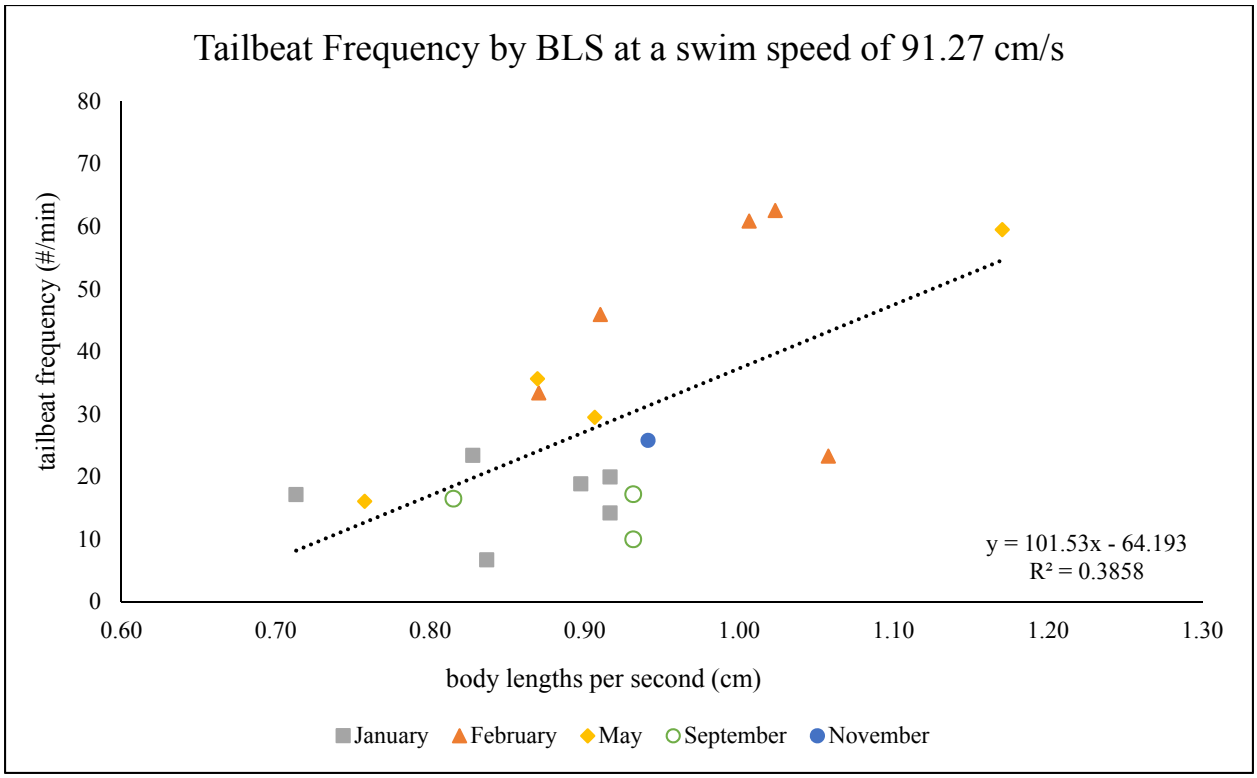

Figure 14. Relationship between tailbeat frequency and body lengths per second at a swimming speed of 91.27 cm/s

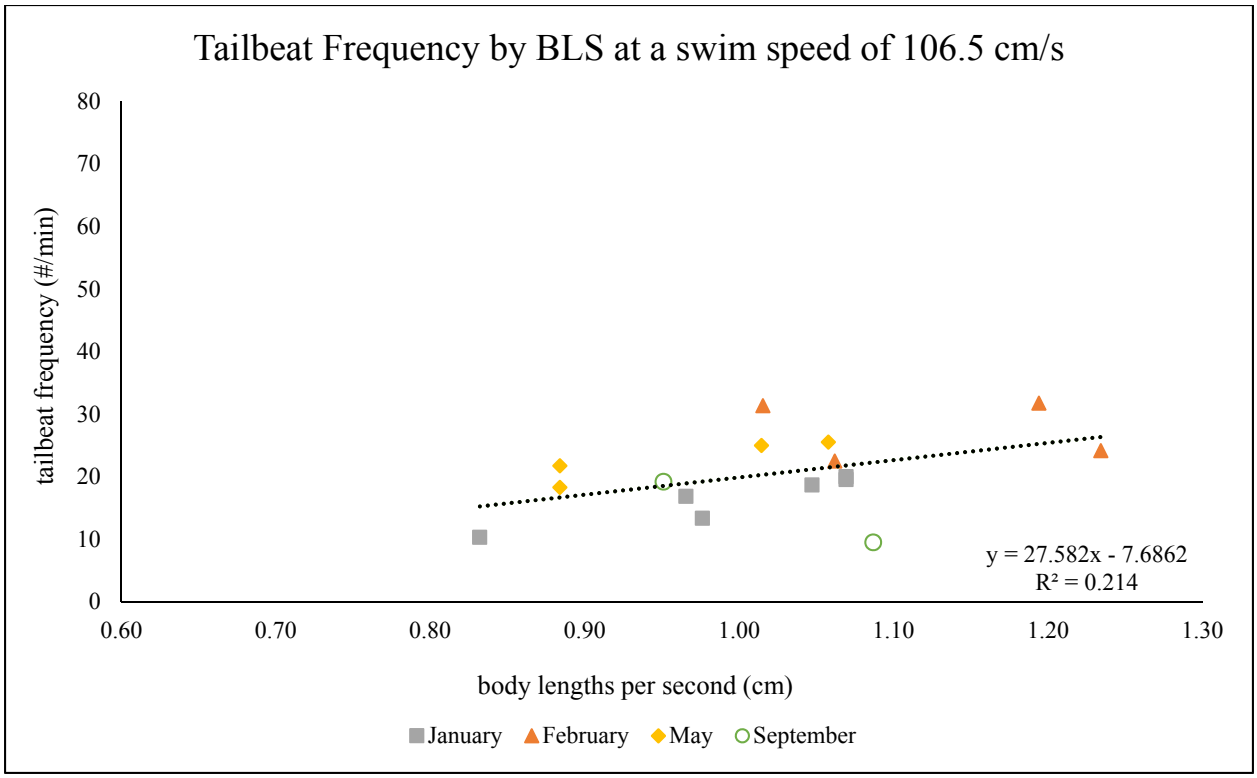

Figure 15. Relationship between tailbeat frequency and body lengths per second at a swimming speed of 106.50 cm/s

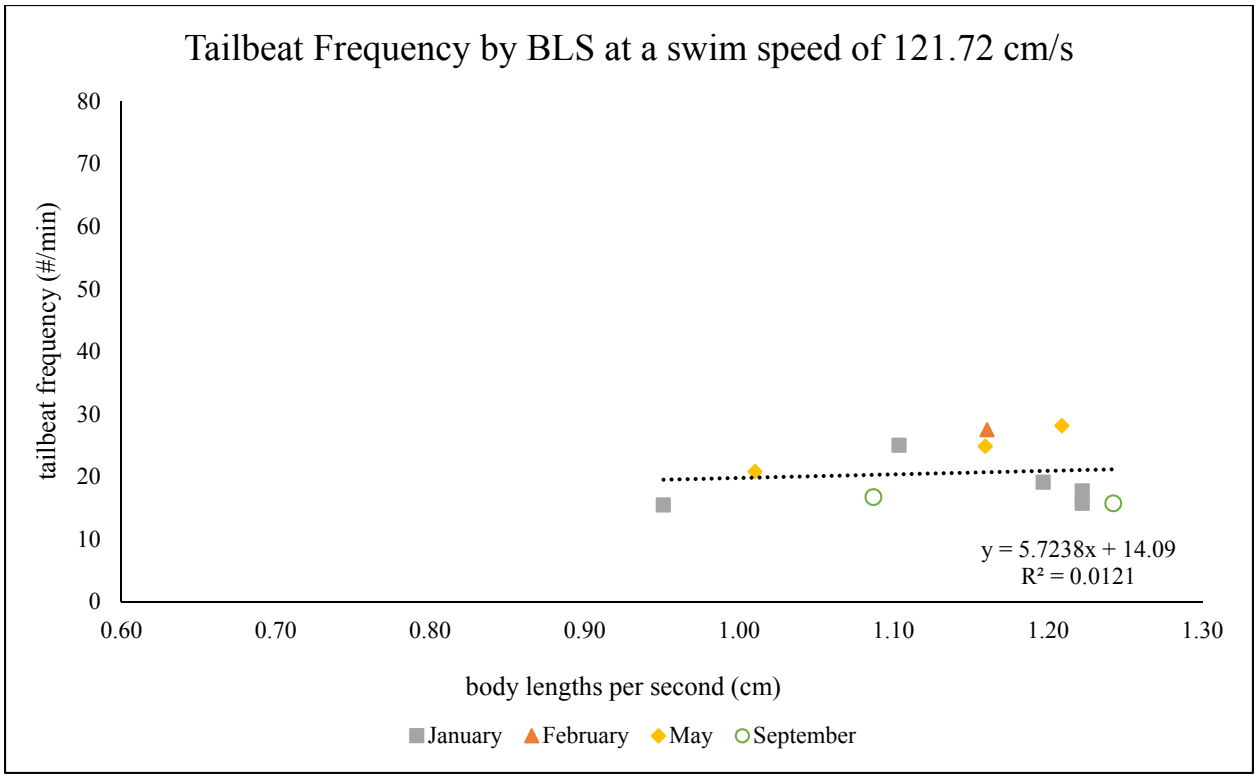

Figure 16. Relationship between tailbeat frequency and body lengths per second at a swimming speed of 121.72 cm/s

Table 16. Average tailbeats per minute by swim speed.

	swim speed (cm/s)			
Month	76.05	91.27	106.5	121.72
Jan	22.08	16.70	16.45	18.60
Feb	43.85	45.21	27.44	27.50
May	43.52	35.19	22.65	24.63
Sept	27.08	14.57	14.35	16.25
Nov	17.83	25.80	--	--

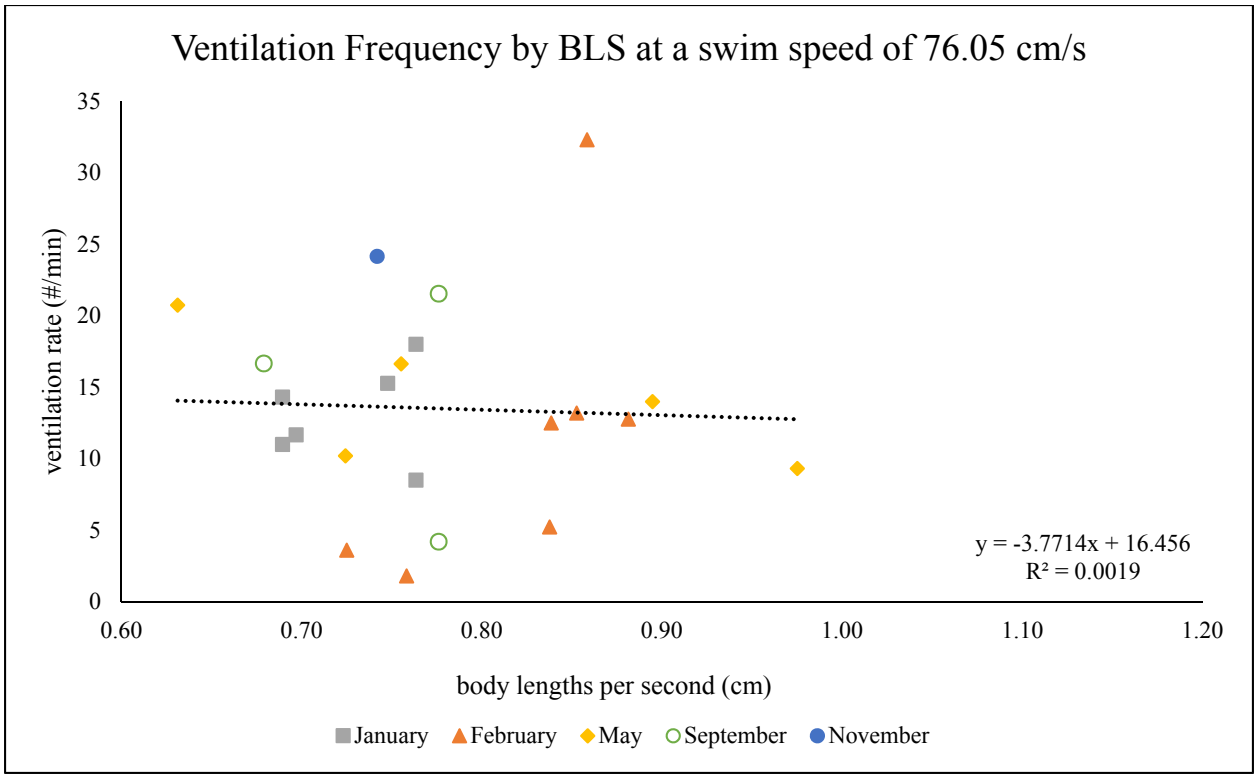

Figure 17. Relationship between ventilation rate and body lengths per second at a swimming speed of 76.05 cm/s

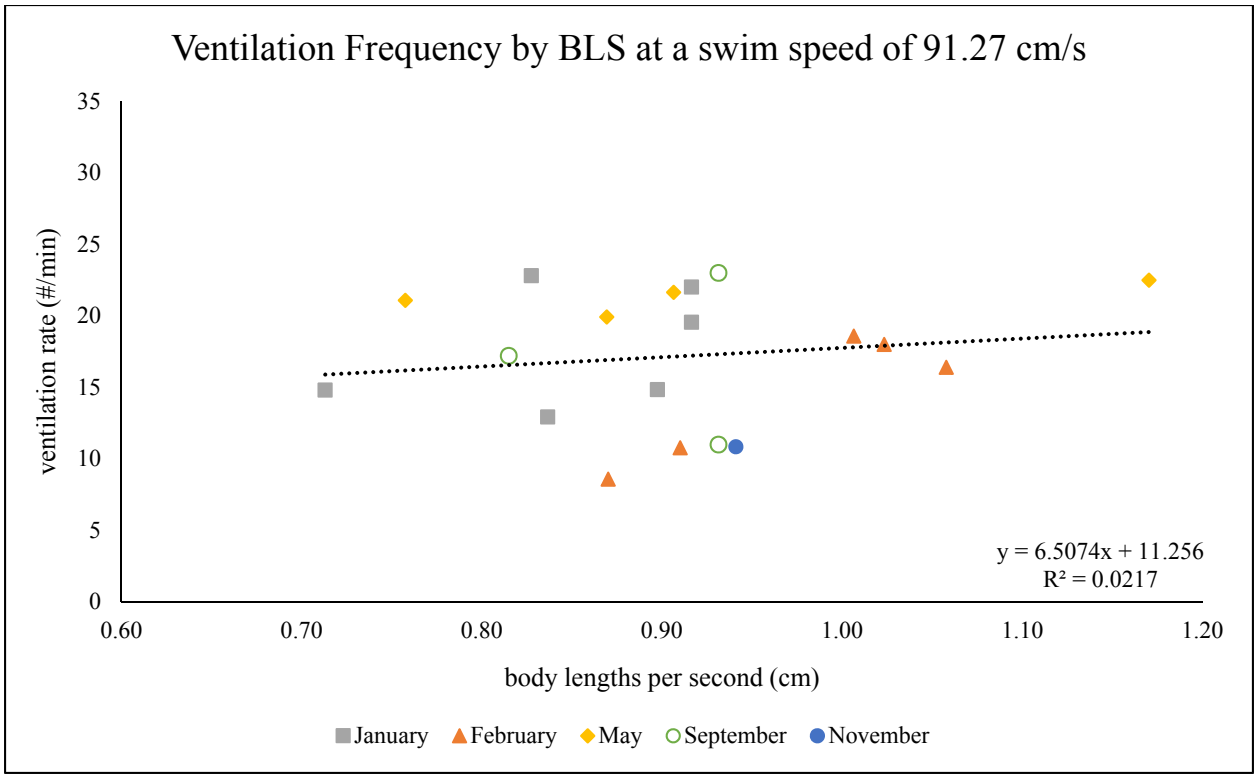

Figure 18. Relationship between ventilation rate and body lengths per second at a swimming speed of 91.27 cm/s

During January and February paddlefish would theoretically filter feed well under threshold regardless of swimming speed (Figure 19; Figure 20). In May zooplankton concentrations began to subside in Moon Lake causing a decrease in suspension feeding efficiency (Figure 21). By September paddlefish in Moon Lake would be suspension feeding at an energetic loss irrespective of the behavioral modification of swimming speed (Figure 22). The results of the cost-to-benefit analysis per season are presented in Table 17.

4. Discussion

This study represents the only direct measurements of an obligate ram-ventilating, filter feeding fish. Paddlefish ranging from 78 -128 cm eye-to-fork length had metabolic rates that ranged from about 50 to 150 mg O_2 kg^{-1} h^{-1} depending on swimming speed and season (Figure 10). This wide range in metabolic rate was not an entirely unexpected result since examined metabolic rates were measured over a large range in body size and weight-specific metabolic rate declines with increasing body size (Schmidt-Nielsen, 1972). However, the weight-specific decrease in metabolic rate with increasing fish size is not as steep in paddlefish as it is in other teleost fishes (Patterson et al., 2013). Patterson et al. (2013) reported a mass exponent of 0.92 as compared with a mass exponent of 0.72 described in other teleost fish (Clarke and Johnston, 1999). The relationship between mass, temperature, and weight-specific metabolic rate for paddlefish routine metabolism was described by the equation $7.66t^{0.979}M^{0.918}$, where, *t* equals temperature in °C and *M* is mass of the fish in kilograms (Patterson et al., 2013). Paddlefish mass may be a more important factor regulating metabolism rather than temperature. The Q_{10} (the measure of the rate of change of a biological or chemical system as a consequence of increasing the temperature by 10 °C) were lower in paddlefish (1.78) than the Q_{10} of other poikilotherms

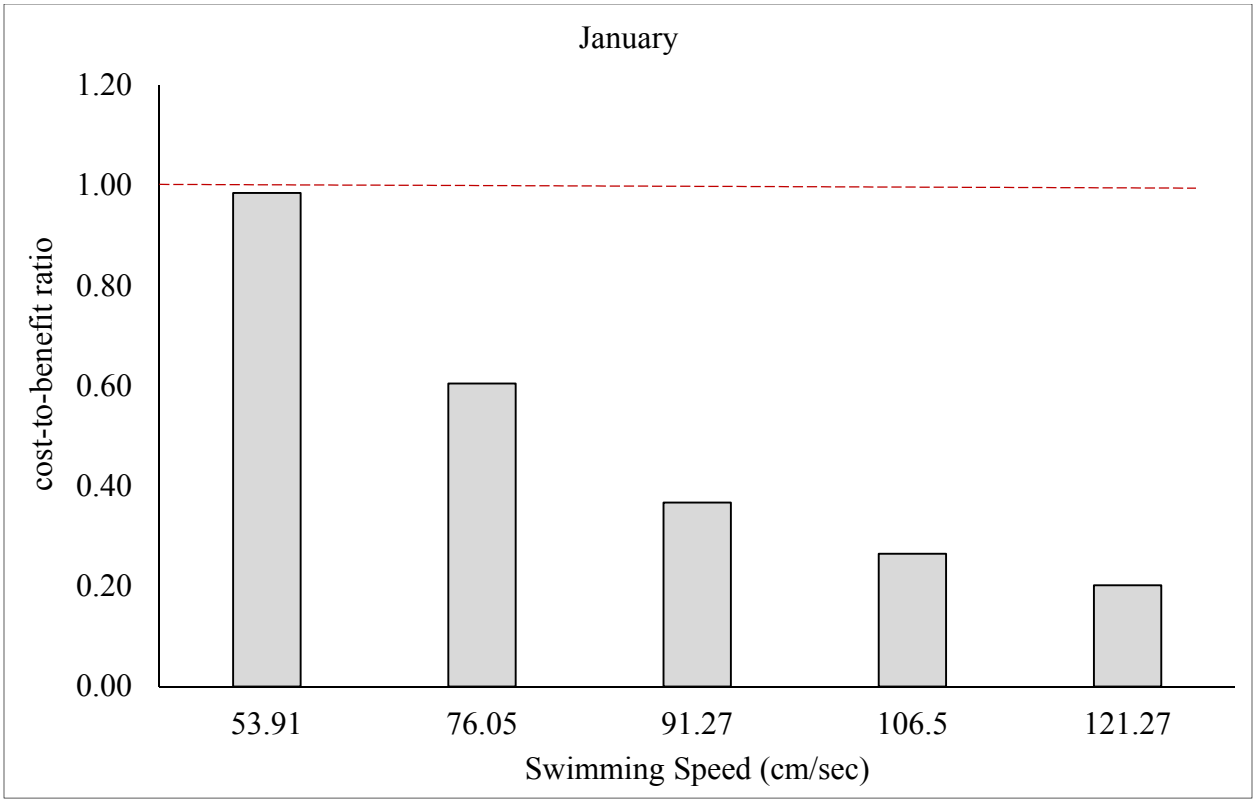

Figure 19. Cost-of-benefit bioenergetics ratio for January 2014

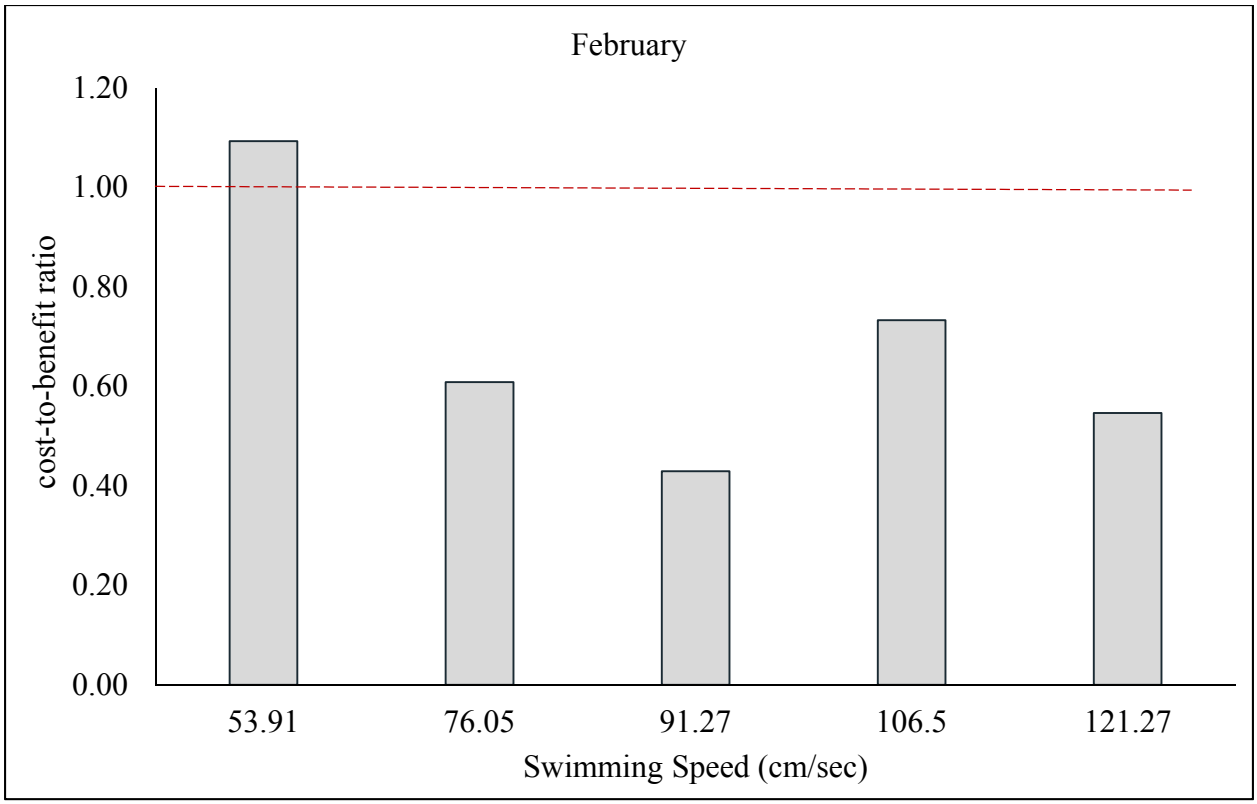

Figure 20. Cost-of-benefit bioenergetics ratio for February 2014

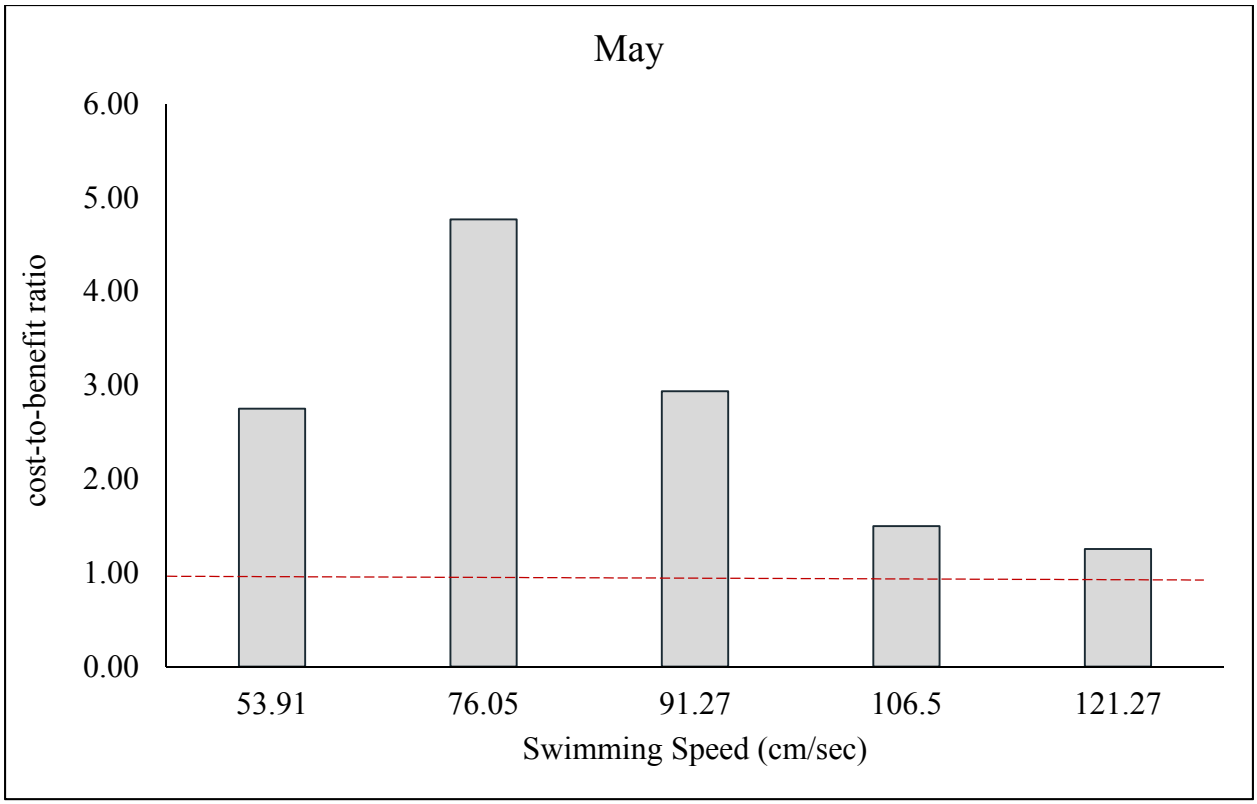

Figure 21. Cost-of-benefit bioenergetics ratio for May 2014

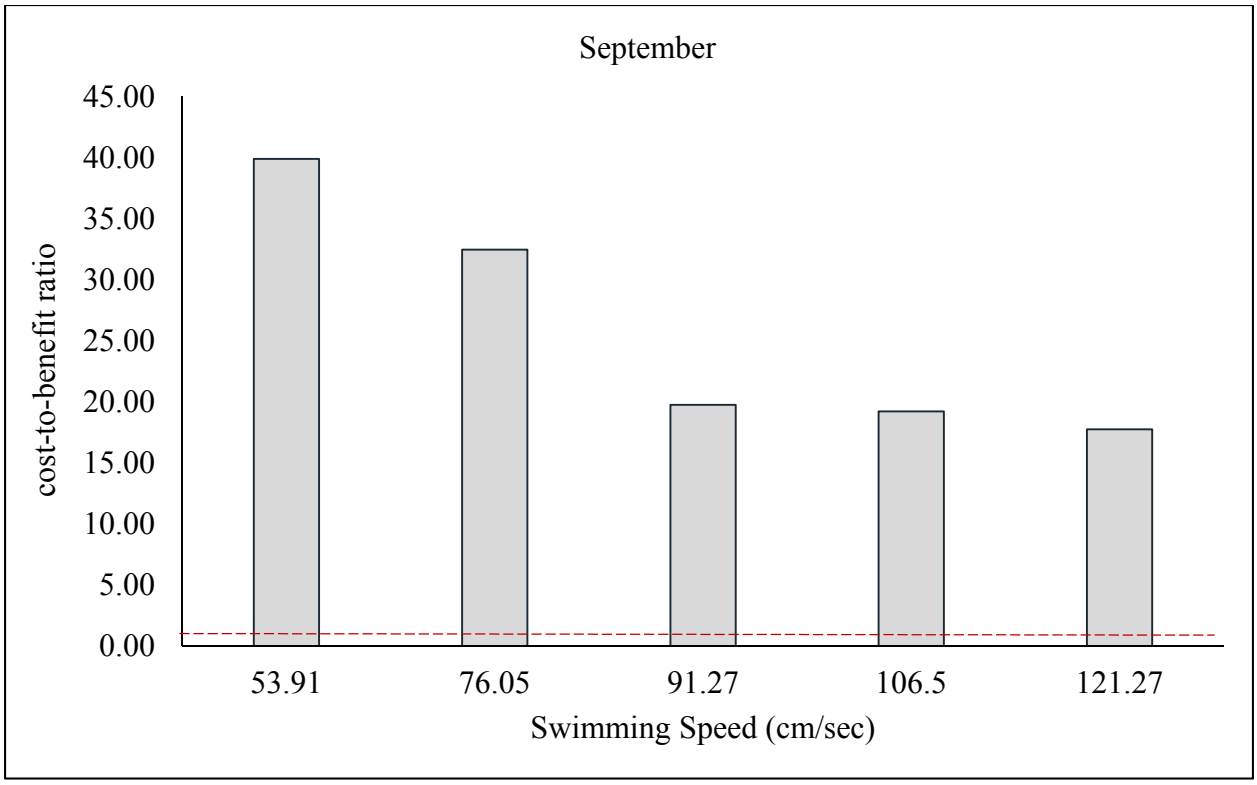

Figure 22. Cost-of-benefit bioenergetics ratio for September 2014

Table 17. Cost-to-Benefit Ratio across Swim Speed and Months

Month	Swimming Speed (cm/s)	Average Cost/Benefit
January	53.91	0.98
	76.05	0.60
	91.27	0.37
	106.5	0.26
	121.27	0.20
February	53.91	1.09
	76.05	0.70
	91.27	0.50
	106.5	0.56
	121.27	0.55
May	53.91	3.13
	76.05	2.70
	91.27	2.90
	106.5	1.42
	121.27	1.18
September	53.91	42.22
	76.05	34.35
	91.27	20.91
	106.5	20.33
	121.27	18.78

(2.0-2.5) (Patterson et al., 2013). This was very similar to the Q_{10} value of 1.68 calculated in this study.

Paddlefish, like most ram ventilators, are efficient swimmers having a lower COT at higher speeds (Carlson, 1998). The lowest cost of transport for paddlefish in this study was between 106.5 and 121.72 cm/s during January, February, May, and September with the optimal swimming speed (U_{opt}) at 116 cm/s for all months as calculated from the fitted power curve. Metabolic rates of paddlefish swimming at routine swimming speeds were similar to the active metabolic rates of paddlefish swimming at 106.50 cm/s in this study. Patterson et al. (2013) reported paddlefish weighing between 11.3 and 12.65 kilograms to have routine metabolic rates of 59.23±4.97, 111.80±6.10, and 202.52±9.03 at 10, 20, and 30°C, respectively. Comparatively, paddlefish in this study weighing between 25.38 and 28.92 kilograms swimming at 106.50 cm/s had similar weight-specific metabolic rates of 56.09±7.25, 106.44±29.68, and 154.68±0.0 at 10.34, 24.30, and 27.0°C, respectively. Paukert and Fisher (2000) reported male paddlefish swimming at speeds up to 4 km/h^{-1} (111 cm/s) in Keystone Reservoir in Oklahoma. Unfortunately, Patterson (2013) did not measure the routine swimming speed associated with routine metabolic rates in their study. However, the field observations of paddlefish swimming during nightly activity in the study by Paukert and Fisher (2000) and the close metabolic rates of similarly sized paddlefish swimming at 106.50 cm/sec in this study, might suggest that paddlefish routinely swim over a narrow range of swimming speeds close to their optimal swimming speed (U_{opt} = 116 cm/sec).

The paddlefish and the basking shark (*Cetorhinus maximus*) are the only two obligate ram ventilating suspension feeders. Information on the critical foraging threshold (zooplankton density g m^{-3} needed to support feeding expenditure) of obligate ram ventilating filter feeders

(paddlefish and basking sharks) is limited. Until recently, empirical evidence of the critical foraging threshold of the basking shark was unknown. Sims (1999) reported that zooplankton densities between 0.48 and 0.70 g m^{-3} were sufficient to support the episodic foraging costs of locomotion in basking sharks. This was much lower than the 1.36 g m^{-3} hypothesized by Parker & Boeseman (1954) which stood as the standard for nearly 45 years (Parker and Boeseman, 1954; Sims, 1999). Sims (2000) reported a best estimate of the metabolic rate of a 5 m basking shark weighing nearly 1000 kg swimming at 0.23 body lengths per second (115 cm/s), to range from 62.5 to 91.1 mg O_2 kg^{-1} h^{-1} ($\bar{x}$ = 80.7±20.1) at temperatures between 13 and 16°C. The more conservative estimate was 23.2 to 192.1 mg O_2 kg^{-1} h^{-1} through a sensitivity analysis. Two paddlefish tested in our study, swimming at 76.05 cm/s at temperatures between 15.06 and 15.79 °C, and weighing 19.5 kg and 23.59 kg had weight-specific metabolic rates of 77.40 and 65.46 mg O_2 kg^{-1} h^{-1}, respectively. These metabolic rates were some of the lowest reported for ram-ventilators.

Like the basking shark, the weight-specific metabolic rates for paddlefish were lower than other continuously active species. Metabolic rates have been measured for a variety of fish species (Parsons, 1990; Carlson et al., 1999; Lowe, 2002). Parsons (1990) reported bonnethead sharks weighing between 0.095 to 4.65 kg had routine metabolic rates at 25°C ranging from 902 to 192.3 mg O_2 kg^{-1} h^{-1}, respectively. Lowe (2002) reported five juvenile scalloped hammerhead shark pups, *Sphyrna lewini*, averaging 570 mm total length had routine metabolic rates of 294 mg O_2 kg^{-1} h^{-1} (96 ± 14.6 kj $kg^{-1}day^{-1}$) while swimming at an average of 0.85 body lengths per second in a Hawaii bay at temperatures ranging from 22 to 29°C. Average metabolic rate of four paddlefish in this study swimming at 0.80, 0.82, 0.93 and 0.93 body lengths per second (91.27

cm/s) at 26.98±0.21°C was 87.31 mg O_2 kg^{-1} h^{-1}. This suggests that basking sharks and adult paddlefish are far more efficient swimmers than other ram ventilating species.

Estimates of the juvenile Pacific Bluefin tuna, *Thunnus orientalis*, (8.8±0.8·kg) swimming at 1 body length per second and at 15°C was 175±29 mg O_2 kg^{-1} h^{-1} (Blank et al., 2007). This was much higher than many migratory species such as salmon and trout, but far lower than it's common relative, the southern Bluefin tuna, *Thunnus maccoyii* (460 mg O_2 kg^{-1} h^{-1} ± 34.9; body mass 19.6±1.9) at a mean water temperature of 19 °C. Comparisons of routine metabolic rates of Pacific Bluefin and Yellowtail tuna of similar mass (7-10 kg) revealed metabolic rates of 222±24·mg·O2·kg^{-1} h^{-1} and 162±19 m O_2 kg^{-1} h^{-1}, respectively, at 20°C (Blank et al., 2007). Similar sized white sharks, *Carcharodon carcharias,* ranging between 137 and 157 cm total lengths had a mean routine metabolic oxygen consumption rate of 246 ± 13 mg O_2 kg^{-1} h^{-1} (Ezcurra et al., 2012). However, metabolic comparisons with Lamniform and Thunniform fishes may be equivocal as these fishes are thermoregulators and retain heat through counter current exchange (rete mirabile).

The apparent lower metabolic expenditure of paddlefish was likewise reflected in the cost of transport analysis. Cost of transport for paddlefish, depending upon speed and season, ranged from about 0.05 to 0.18 cal/g/km. These values are lower than those reported for other species. Reported cost of transport of juvenile bonnethead sharks weighing < 9 kg were greater than 0.38cal/g/km (Parsons, 1990). The smallest shark in the study, weighing 95 grams, had an estimated cost of transport of 1.21 cal/g/km. In paddlefish, there was a decrease in cost of transport (increased swimming efficiency) with increasing swim speed (Figure 12) and fish mass (kg) (Figure 11). A similar increase in swimming efficiency with increasing swim speed was observed in the blacknose shark, *Carcharhinus acronotus* (Carlson, 1998). Blacknose sharks

decreased the COT from 1.68 cal/g/km at 25 cm/s to 0.9 cal/g/km at 39 cm/s at 27±3°C. Paddlefish in this study reduced their COT from 0.11 cal/g/km at 76.05 cm/s to 0.07 cal/g/km at 121.72 cm/s at 26.98±.11°C. The low metabolic rate observed in paddlefish and basking sharks might be an adaptation to the filter feeding strategy. Obviously, minimizing metabolic expenditure would result in a decreased cost/benefit ratio (low values equivalent to higher efficiencies) during filter feeding. It is possible that the highly efficient swimming of paddlefish is an adaptation to the low potential energy gain that results from filter-feeding in low productivity environments. The highly migratory nature of this species and the necessity to engage in extended spawning migrations that likely take the species into low productivity areas has resulted in adaptations to increase swimming efficiency.

An extremely interesting aspect of this research was the results of the cost-to-benefit analysis. To this researcher's knowledge, no study has reported cost-to-benefit values for any filter feeding species. For the months of January and February, cost-to-benefit ranged from about 0.20 to 1.09 (Table 17). During winter, cost was only 20 to 109% of benefit. However, a small increase in cost in May was followed by a large increase in September. Although respiration rate measurements were not available in summer months, these data suggest that cost likely began to approach and perhaps exceed benefit during those months and by September cost averaged around 200 to 400% of benefit. It is noteworthy that paddlefish were observed to exit Moon Lake beginning in late April in both 2013 and 2014. The latest a tagged fish remained in the lake was late July. Most left the lake in April or June. It is unknown if these paddlefish returned the following year; however, at least two of the fish from 2013 made long excursions into the Missouri River over 2,776 kilometers away.

The cost of transport relationship for paddlefish in Moon Lake suggests that their swimming efficiency is highest (cost/benefit ratio lowest) when fish attain a size of between 20 and 25 kg (980 to 1049 mm EFL) (Figure 11). This is larger than the size at maturity of paddlefish reported in the Alabama River (650 mm EFL), but are consistent with size and weight at maturity for paddlefish populations in Lake Pontchartrain (Reed et al., 1992; Hoxmeier and Devries, 1997). It is clear from this study that at least a portion of the paddlefish population leave Moon Lake in summer when zooplankton resources are at a yearly low. It is unclear if all fish leave the lake at this time, but it is possible that the reduction in zooplankton provides a cue for fish to depart. Smaller fish with lower swimming efficiency may stay in the lake or move shorter distances out of the lake in search of better grazing waters. The largest fish, those with the highest absolute energy requirements, cannot remain in the low energy environment that exists during summer. These fish are mature at about the time when they are best prepared (highest swimming efficiency) for a long distance migration. In similar fashion, Parsons (1990) reported that in the bonnethead shark, *Sphyrna tiburo,* mature sharks have the lowest cost of transport (highest efficiency) and "the relatively low efficiency of the locomotory system in juveniles may preclude them from participation in extensive migrations". It is clear from this study that paddlefish engage in an extensive migration that is likely reproductive in nature. On two occasions, paddlefish tagged in Moon Lake were captured by fisherman in the Missouri River near Levasy, MO and Yankton, SD (Gavins Point Dam) nearly 2087 and 2,776 kilometers away, respectively. Apparently, paddlefish movement between the upper and lower Mississippi River has been going on for some time. Rosen et al. (1982) reported that a paddlefish from the same area (Yankton, SD) made a similar trip down the Mississippi River and was caught near Memphis, Tennessee.

The story that is unfolding regarding paddlefish in Moon Lake and perhaps in many oxbows along the Mississippi River is that these waters represent important grazing areas where fish over-winter and engage in pre-migratory fattening. The phenomenon of pre-migratory fattening has been well documented in a variety of species such as the golden topminnow, *Fundulus chrysotus*, hummingbirds, and snow buntings (Lee and Meier, 1967; Banks et al., 1989; Suarez, 2013) and serves to prepare organisms for the energetic challenge of migration. The challenge faced by Moon Lake paddlefish is a heretofore unreported migration of epic proportions, travelling thousands of kilometers for spawning.

5. Conclusions

The results presented here suggest that Moon Lake is an important energetic sanctuary for paddlefish. The plankton rich waters of this oxbow (Chapter 2), and perhaps many other oxbows along the Mississippi River, provide an important staging area where paddlefish may fatten prior to engaging in an extensive spawning migration. The cost-to-benefit analysis reveals that during much of the growing season paddlefish are feeding efficiently with a surplus of calories to support growth and reproduction. During early reproductive development paddlefish invest energy into the production of gonadal fat bodies, energy reserves used up over their first several spawning migrations. Scarnecchia (2007) reported that migration distance is inversely proportional to gonadal fat body mass. The gonadal fat bodies are quickly depleted in females over several spawns while the depletion is more gradual in males. Mature paddlefish in the "prime reproductive" period grow very little as mature adults and place the majority of energy investments into gonadal recrudescence. Recrudescence may take between one and two years and results in an annual gap in spawning periodicity (Scarnecchia et al., 2007).

Two species of Asian carp, the bighead (*Hypophthalmichthys nobilis*) and the silver carp (*Hypophthalmichthys molitrix*) are two invasive species that directly compete with paddlefish for available food. Since this study in Moon Lake began, both species have made their way into Moon Lake. In 2012 only one silver carp was caught as by-catch as opposed to nearly 60 over the next two years. During the commercial paddlefish harvest in 2014 a bighead carp weighing 49.44 kilograms (190 lbs.) with over 25 kilograms (55 lbs.) of eggs was caught in Moon Lake. The high fecundity and relative numbers of both bighead and silver carp make it a real threat to paddlefish populations throughout the region and their impact may cause a reduction in paddlefish numbers as high as 15% across the lower Mississippi River (Jan Hoover, personal communication).

This study has shown that a reduction of zooplankton abundance over season might cause movement of paddlefish from the lake. As more carp move into the area, competition may depreciate zooplankton abundance. There are two possible scenarios. If paddlefish are cued to leave due to less than optimal feeding conditions (due to competition) than the paddlefish populations may be okay. If resources are diminished early in the growing season than paddlefish will have ample time to the exit the lake and find other resourceful areas with suitable prey. The paddlefish growth may be reduced, but the impact may not be appreciable. On the other hand, if paddlefish are not cued to leave by zooplankton abundance, but rather are cued by other biotic and abiotic cues than the situation may be more severe. The paddlefish will remain in Moon Lake where competition is high. Without leaving the lake, competition may reduce energy reserves to significant levels. Paddlefish will not have time to accumulate needed lipid reserves before entering into pre-spawning migrations and fecundity (reproductive potential), in the long run, might be reduced.

Paddlefish populations need to be closely monitored and a premium needs to be placed of conservation of backwater habitats and oxbow lakes. Overharvest, competition, waterway development, and pollution have placed strain on paddlefish populations and if not closely managed paddlefish may be in peril.

CHAPTER IV

THE AMERICAN PADDLEFISH, *POLYODON SPATHULA*, IN MOON LAKE, MISSISSIPPI: MOVEMENT AND HABITAT USE

1. Introduction

Animal movement is important to growth, survival and reproductive success (Kahler et al., 2001). Swimming performance in fish is affected by oxygen tension, photoperiod, water depth, turbidity, gas/nutrient transport and exchange, and temperature. Temperature is the most important factor affecting both the rate of metabolic reactions, as well as, regulating the dissolved oxygen concentrations of water. As water temperatures warm seasonally, the scope of activity (metabolic range) increases, and fish become more active. As the scope of activity increases home range of fish will expand (Warden and Lorio, 1975; Diana, 1995; Jobling, 1995).

Paddlefish move over long distances, but often take seasonal residence in oxbows to take advantage of slow currents, deeper waters, and plentiful prey (Hoxmeier and Devries, 1997). Oxbows often have rich resources of zooplankton that provide an energetic savings during seasonal periods. The duration of residence, movements within the basin, and prey availability are all dynamic and change in response to environmental conditions and will affect energetic balance, foraging success, and growth and reproduction (Schoener, 1971; Kahler et al., 2001). It stands to reason that the duration of residence will continue as long as it is beneficial to do so. It may be that paddlefish remain in oxbows during poorer conditions at an energetic loss, but that the energetic savings gained during profitable periods outweighs the energetic loss during harsher environmental conditions.

A profile of depth and habitat use in paddlefish has not been examined on a micro scale. Moon Lake is a relatively small lake (2,200 acres) with the deepest sections limited to an area of roughly 0.45 km^2. Because paddlefish prefer deep water habitat (Jennings and Zigler, 2009), a limited resource, it is of interest to understand the habitat partitioning among paddlefish in Moon Lake.

Paddlefish are often observed with traumatic injury to their rostrum, resulting in damage and a significant reduction to the number of sensory receptors (Ampullae of Lorenzini) on their rostrum. The area and shape of paddlefish rostra differ among individuals, and those with larger rostral areas may have an advantage over others as they may have an increased ability to detect zooplankton. Likewise, rostral shape may have a role in swimming efficiency by affecting drag and hydrodynamics. Rostral shapes range between spatulate and rectangular. Spatulate rostra are thinner at the base and wider at the tip while rectangular rostra have a more consistent width from base to tip.

Moon Lake is located in northwest Mississippi in the flat agricultural delta. The area is characteristic of producing high prevailing winds. High directional winds may influence the distribution of zooplankton by limiting their swimming ability and normal grazing patterns. Strong, consistent winds may aggregate zooplankton into dense pockets that may increase foraging efficiency in paddlefish. The degree may depend on fetch, duration, wind speed, direction, temperature, and the area of the lake affected. It is reasonable that paddlefish might spend more time in areas of higher zooplankton concentrations thus increasing foraging efficiency. The long narrow unabated channel running north and south will act as a corridor, channelizing wind and will most likely have the most pronounced effect on paddlefish distribution. In addition, the effect of Alcorn Island will aggregate fish and resources in the large

area to the north and northeast of the island when prevailing winds are south to southwesterly. Winds from the north or northwest may act to produce currents through the narrow northern neck of Moon Lake causing a redistribution of paddlefish in the northern or southern ends.

The objectives of this study were to: 1) construct a bathymetry map for Moon Lake, 2) describe the daily and seasonal movements of paddlefish in Moon Lake, 3) characterize the daily and seasonal use of habitat (i.e. depth and location) of paddlefish 4) examine the effect of rostrum size and shape on paddlefish movement and foraging success, and 5) determine if habitat use of paddlefish (depth and location) correlates with wind speed, wind direction, relative humidity, barometric pressure, and temperature.

2. Material and Methods

Lake Bathymetry and Lake Sections

Lake depth measurements were recorded using a Garmin echoMap50 Chart plotter and transducer attached to a 19' McKee Craft boat. Records were sampled at 10 second intervals to an internal microSD card. Thirty-nine thousand three hundred and forty-six (39,346) measurements were recorded during tracking events. An additional two thousand three hundred and eighty (2,380) GPS waypoints were taken at equidistance intervals around the perimeter of Moon Lake and Alcorn Island. Data points were entered into a Microsoft® Excel spreadsheet and transferred to ArcCatalog® GIS software. All depth points were converted and stored in a geodatabase in the form of an ArcGis® point feature class. Using the Inverse Distance Weight (IDW) Interpolation Geoprocessing Tool, a bathymetric map raster layer was constructed (Figure 23).

Moon Lake was divided into 9 subdivisions: north upper, north lower, middle upper, middle lower, Alcorn upper, Alcorn left, Alcorn right, Alcorn lower, and south tip (Figure 24).

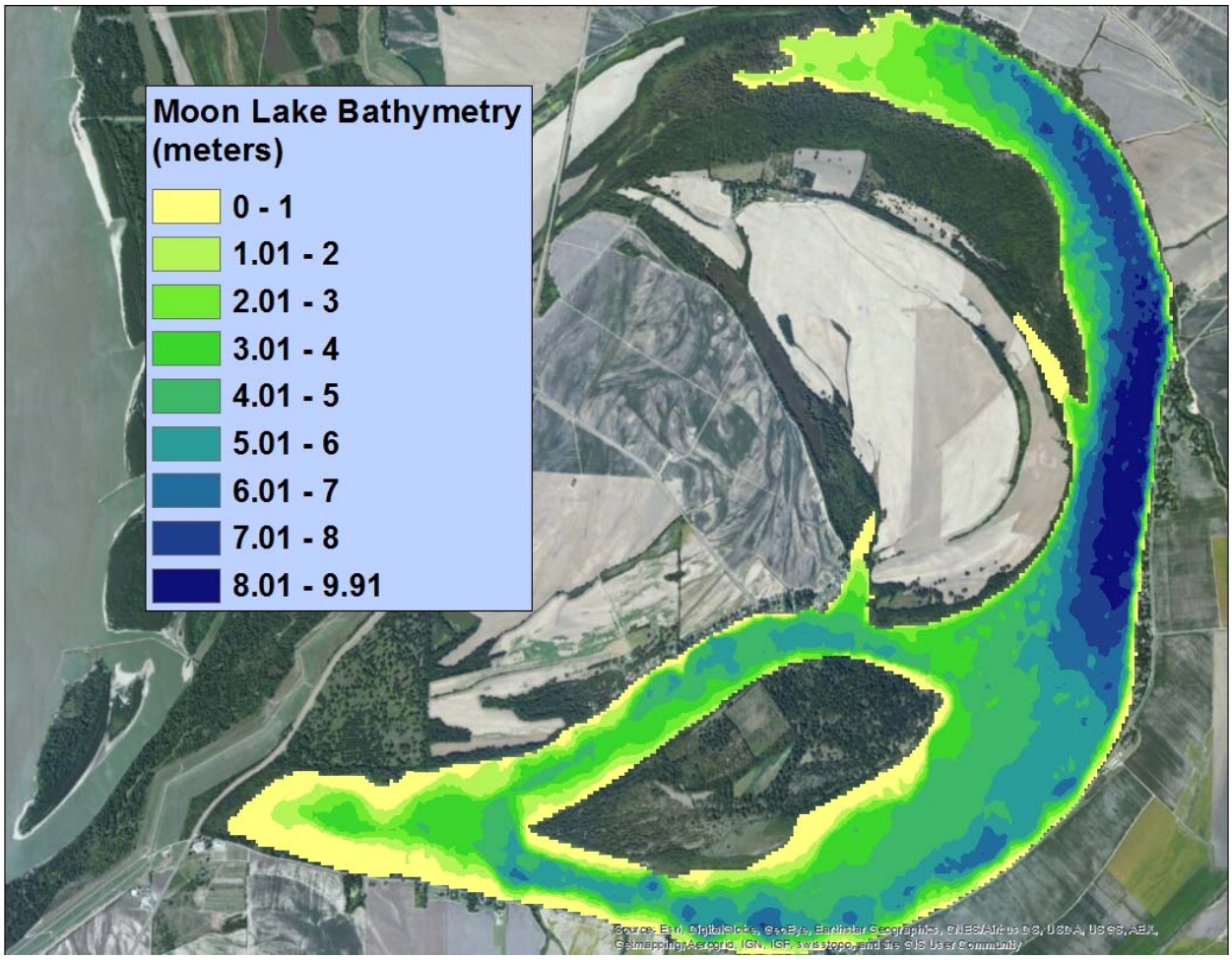

Figure 23. Moon Lake Bathymetry

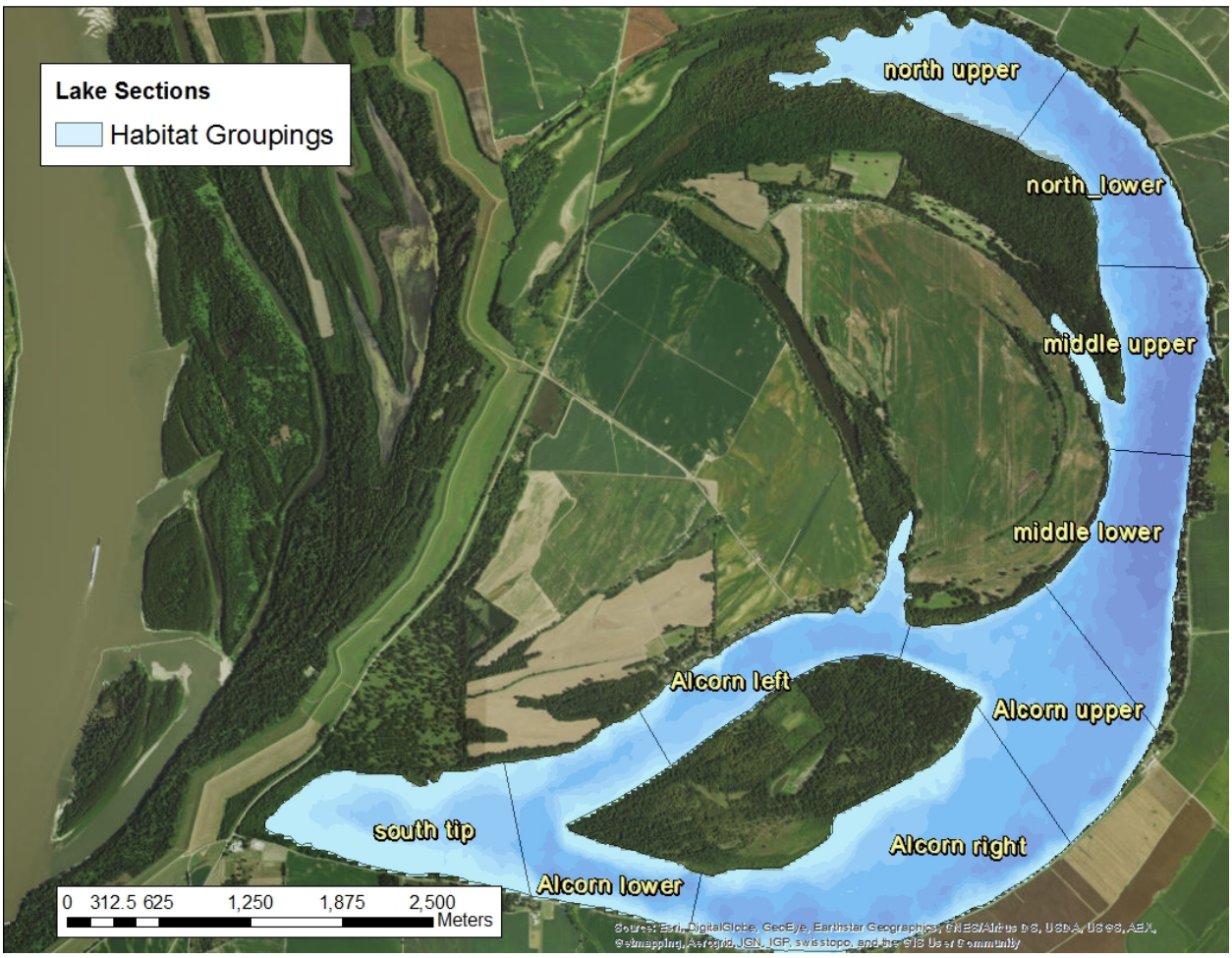

Figure 24. Lake Sections

Lake sections varied in location, basin morphology, and percent depth. Sections were used as landmarks to describe and characterize differences in habitat use.

Telemetry

A total of twenty-six paddlefish were captured from Moon Lake in northwest Mississippi using floating gillnets over a span of two years from November 2012 to September 2014. Paddlefish were weighed in kilograms and eye-to-fork-length, rostral length, mouth width, and mouth height were measured to the nearest millimeter. The Fulton's condition factor was calculated as the ratio of fish weight (kg) to eye-to-fork length cubed. Fish with defective rostra were noted and photographed.

The first paddlefish in this study was caught on November 7, 2012 and was fitted with a F2200 radio transmitter produced by Advanced Telemetry Systems. Transmitters were placed on four additional fish on March 21, 2013 with the help of Garry Lucas from the Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP). This group of five paddlefish was tracked using radio telemetry for three months ending on June 21, 2013.

On January 14 and 15 of 2014, eleven paddlefish were tagged with the help of members of the US Army Engineer Research and Development Center from Vicksburg, Mississippi. The paddlefish rostra of these eleven were imaged and imported into Adobe Photoshop to measure rostrum area. Rostra with significant damage were noted. While all eleven fish were fitted with radio transmitters (F2200) only seven of the eleven received an additional LAT 1400 data logger from Lotek wireless®. LAT 1400 data loggers recorded depth and temperature every 2 minutes and 20 seconds. All radio transmitters and data loggers were mounted to the soft fleshy portion of the dorsal fin using 50 lb. monofilament line (Figure 25). The eleven fish were tracked during February, 2014. All eleven fish were recaptured during the commercial paddlefish harvest held at

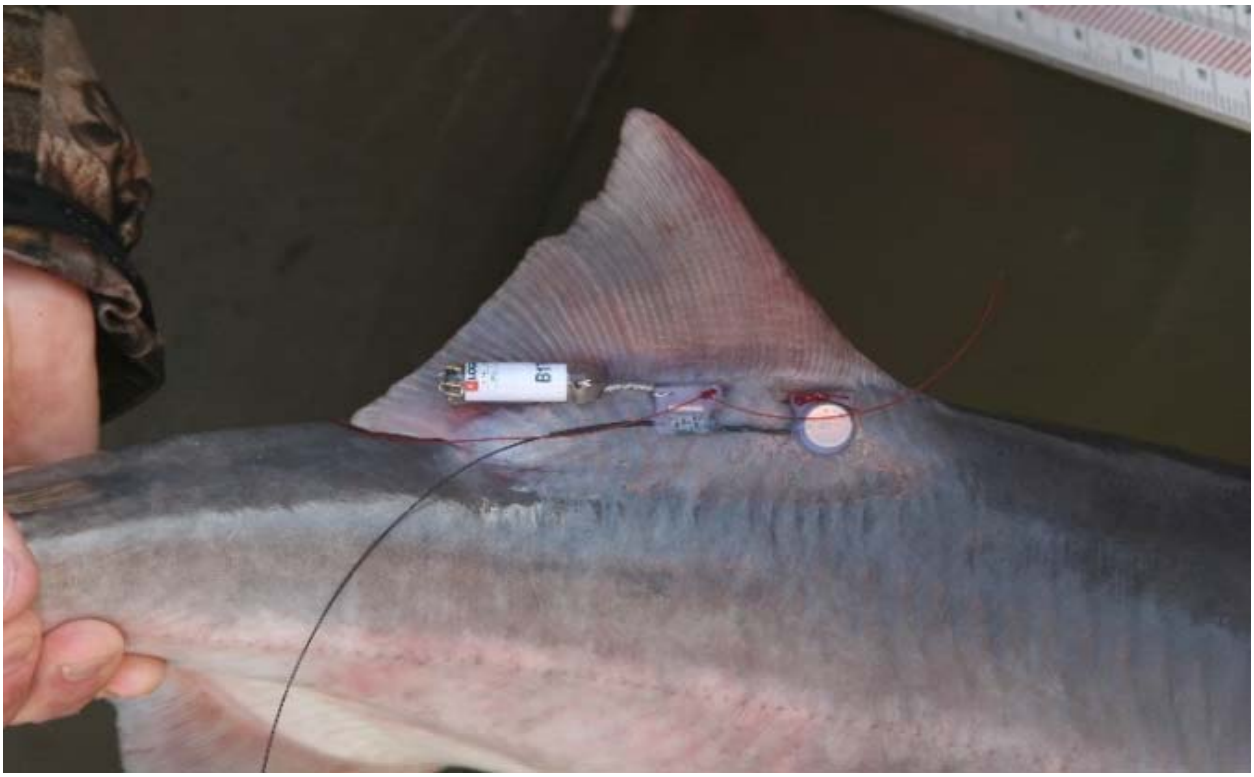

Figure 25. F2200 Radio Transmitter and LAT 1400 Data logger attached to the soft dorsal area using 50lb. monofilament

Moon Lake from February 24 to 28, 2014. Data were retrieved and downloaded from the archival data loggers.

Four fish were tagged with radio transmitters and data loggers over an eight day period beginning on March 22, 2014. Of these four, one was never relocated, two were tracked until mid-April, and the fourth was tracked until May 19, 2014. An additional three paddlefish were tagged on May 3, 2014 including one fish that was fitted not only with a radio transmitter and data logger, but also was the first to receive the fish ichthyometer (Chapter 5, Figure 26). The ichthyometer recorded swimming speed in centimeters per second. This fish was tracked periodically over 16 days before being recaptured with a floating gill net on May 19, 2014. The other two fish were tracked through mid-June and the last part of July, respectively. Three of the last four fish tagged during this study were never relocated. On September 1, 2014 the last of the twenty-six fish were tagged with all three electrical devices: radio transmitter, data logger, and ichthyometer (Figure 26). The fish was tracked for 16 days until the ichthyometer detached from the fish on September 17, 2014. A total of twelve waypoints were taken during the day and thirteen waypoints were taken at night.

Fish were tracked and monitored using a 19 foot McKee Craft boat as often and as long as weather and schedule permitted. Using a R2100 receiver from Advanced Telemetry Systems and a handheld Garmin Rino 655t GPS unit or a Garmin echoMap50 Chart plotter, the fish coordinate position was recorded in decimal degrees using the NAD 1983 geographic coordinate system. East and west transects were followed by boat following a square wave pattern north or south until an acoustic signal was received by the low frequency antenna. The audio gain was reduced in close fish proximity to hone the signal. Locations with the loudest acoustic reception were marked as a fish waypoint.

Figure 26. Ichthyometer

The location and distance moved in meters was measured and recorded as the minimal linear distance per unit time between GPS waypoints (latitude/longitude) and later analyzed on ArcGis® computer software from Environmental Systems Research Institute (ESRI). Archival and weather data were aligned with geospatial paddlefish locations through key time signatures. The twenty-six fish were located a total of 525 times over the twenty-four month study period.

Meteorological Effects on Movements

A Kestrel 4500 weather meter (Figure 27) was deployed in Moon Lake at 34.43299° latitude and -90.49841° longitude onto a stationary pylon using a gorilla tripod and Kestrel weather vane. Measurements were taken simultaneously with telemetry tracking. Measurements included wind direction, wind speed (m/s), barometric pressure (mmHg), relative humidity (%), and temperature (°C). Wind direction was calculated as a percentage over time to identify periods of strong winds of a single directionality. Periods of time when wind direction and strength were consistent were overlaid with patterns of movement and behavior of paddlefish.

Zooplankton Sampling

Materials and methods are outlined in detail in chapter 2. The differences in caloric values of zooplankton collected between fish sites and random sites were compared, as well as, determining if a correlation exists between rostrum areas (size) and number of total calories per cubic meter sampled at each fish location.

Figure 27. Kestrel 4500 weather meter and weather vane

3. Results

Bathymetry

Moon Lake has a maximum depth of 10.2 meters and during this study, an annual temperature range between 2 and 32.7°C. Average depth and temperature in 2013 was 5.6 meters and 21.25°C, respectively. In 2014 the average depth was slightly higher at 6.05 meters. Average temperature through July of 2014 was 10.6°C. The deepest area of Moon Lake is a 0.40 square kilometer area that runs parallel to the eastern shoreline and was once the old bend of the Mississippi River. The northern boundary starts at the Yazoo Pass and extended southward for 2.04 kilometers before gradually sloping up to 4 to 6 meters just east of the northern tip of Alcorn Island (Figure 23). The northern and southern sections are the shallowest areas and ranged in depths from 0 to 4 meters. Deeper pockets occurred scattered on the bottom along the southeastern bend.

Paddlefish Movements in 2012 to 2013

One paddlefish was caught in 2012 and four in 2013. This group of fish was tagged only with radio transmitters, therefore, only latitude and longitude were recorded. The first paddlefish in the study was caught on November 7, 2012. Named *"Copeia"*, the fish was located a total of sixty-four times between November of 2012 and April of 2013 (Table 18; Table 19; Table 20). *Copeia* stayed in deeper water areas during the fall months when temperatures were around 2 to 3 degrees ($\bar{X} = 2.49$), and rarely ventured into shallower waters less than 3 meters during the fall (Figure 28). Broader excursions occurred during the spring when temperatures began to rise ($\bar{X} = 15.31$°C). *Copeia* was discovered more often in the northern section of the lake as opposed to the middle sections. Although *Copeia* was captured in the southeastern portion of the lake, not a single location was reported from this area following capture. Most waypoints were taken during

Table 18. Waypoint information for Copeia in November and December of 2012

Month - Day	Map ID	Time	Paddlefish ID	Lake Section	Lake Depth (m)
Nov/17/2012	1	16:19:11	COPEIA	Alcorn upper	--
Nov/30/2012	2	14:45:08	COPEIA	Middle lower	--
Nov/30/2012	3	15:01:19	COPEIA	Middle upper	--
Nov/30/2012	4	15:29:47	COPEIA	Middle lower	--
Nov/30/2012	5	15:34:57	COPEIA	Middle lower	--
Nov/30/2012	6	15:37:48	COPEIA	Middle lower	--
Nov/30/2012	7	15:46:31	COPEIA	Middle lower	--
Nov/30/2012	8	15:55:57	COPEIA	Middle lower	--
Nov/30/2012	9	16:22:24	COPEIA	Middle lower	--
Nov/30/2012	10	16:28:18	COPEIA	Middle lower	--
Dec/01/2012	11	15:01:02	COPEIA	Middle lower	--
Dec/01/2012	12	15:51:18	COPEIA	Middle lower	--

Table 19. Waypoint information for Copeia in January of 2013

Month - Day	Map ID	Time	Paddlefish ID	Lake Section	Lake Depth (m)
Jan/11/2013	13	14:54:31	COPEIA	Middle upper	--
Jan/11/2013	14	15:00:36	COPEIA	Middle upper	--
Jan/11/2013	15	15:01:14	COPEIA	Middle upper	--
Jan/11/2013	16	15:01:30	COPEIA	North lower	--
Jan/11/2013	17	15:02:45	COPEIA	North lower	--
Jan/11/2013	18	15:12:19	COPEIA	North lower	--
Jan/11/2013	19	15:15:19	COPEIA	North lower	--
Jan/11/2013	20	15:18:40	COPEIA	North lower	--
Jan/11/2013	21	15:19:24	COPEIA	Middle upper	--
Jan/11/2013	22	15:27:00	COPEIA	North lower	--
Jan/11/2013	23	15:27:19	COPEIA	North lower	--
Jan/11/2013	24	15:34:17	COPEIA	Middle upper	--
Jan/11/2013	25	15:36:09	COPEIA	Middle upper	--
Jan/11/2013	26	15:36:13	COPEIA	Middle upper	--
Jan/11/2013	27	15:36:40	COPEIA	Middle upper	--
Jan/11/2013	28	15:37:51	COPEIA	Middle upper	--
Jan/11/2013	29	15:38:40	COPEIA	Middle upper	--
Jan/11/2013	30	15:39:12	COPEIA	Middle upper	--
Jan/11/2013	31	15:48:30	COPEIA	Middle upper	--
Jan/11/2013	32	15:48:33	COPEIA	Middle upper	--
Jan/11/2013	33	15:49:45	COPEIA	Middle upper	--
Jan/11/2013	34	15:50:35	COPEIA	Middle upper	--
Jan/11/2013	35	15:54:58	COPEIA	Middle upper	--
Jan/11/2013	36	16:07:15	COPEIA	Middle upper	--
Jan/11/2013	37	16:14:58	COPEIA	Middle upper	--

Table 20. Waypoint information for Copeia in spring of 2013

Month - Day	Map ID	Time	Paddlefish ID	Lake Section	Lake Depth (m)
Mar/16/2013	38	11:53:01	COPEIA	North lower	--
Mar/16/2013	39	11:56:17	COPEIA	North lower	--
Mar/16/2013	40	11:56:25	COPEIA	North lower	--
Mar/16/2013	41	13:08:23	COPEIA	North upper	--
Mar/16/2013	42	13:29:58	COPEIA	North lower	--
Mar/16/2013	43	13:30:52	COPEIA	North lower	--
Mar/16/2013	44	15:07:31	COPEIA	North upper	--
Mar/16/2013	45	15:08:56	COPEIA	North upper	--
Mar/16/2013	46	15:24:02	COPEIA	North upper	--
Mar/16/2013	47	15:24:21	COPEIA	North lower	--
Mar/16/2013	48	15:30:39	COPEIA	North upper	--
Mar/16/2013	49	15:30:49	COPEIA	North upper	--
Mar/28/2013	50	17:37:23	COPEIA	North lower	--
Mar/28/2013	51	17:53:58	COPEIA	North lower	--
Mar/28/2013	52	17:54:21	COPEIA	North lower	--
Apr/06/2013	53	03:53:13	COPEIA	Alcorn upper	--
Apr/06/2013	54	05:06:59	COPEIA	Alcorn upper	--
Apr/06/2013	55	05:53:12	COPEIA	Alcorn upper	--
Apr/06/2013	56	06:04:17	COPEIA	Alcorn upper	--
Apr/06/2013	57	06:05:35	COPEIA	Alcorn upper	--
Apr/06/2013	58	07:50:50	COPEIA	Alcorn upper	--
Apr/21/2013	59	09:34:45	COPEIA	North upper	--
Apr/21/2013	60	12:19:25	COPEIA	North lower	--
Apr/21/2013	61	12:22:54	COPEIA	North lower	--
Apr/21/2013	62	12:54:10	COPEIA	North lower	--
Apr/25/2013	63	08:09:49	COPEIA	North upper	--
Apr/25/2013	64	11:25:03	COPEIA	North upper	--

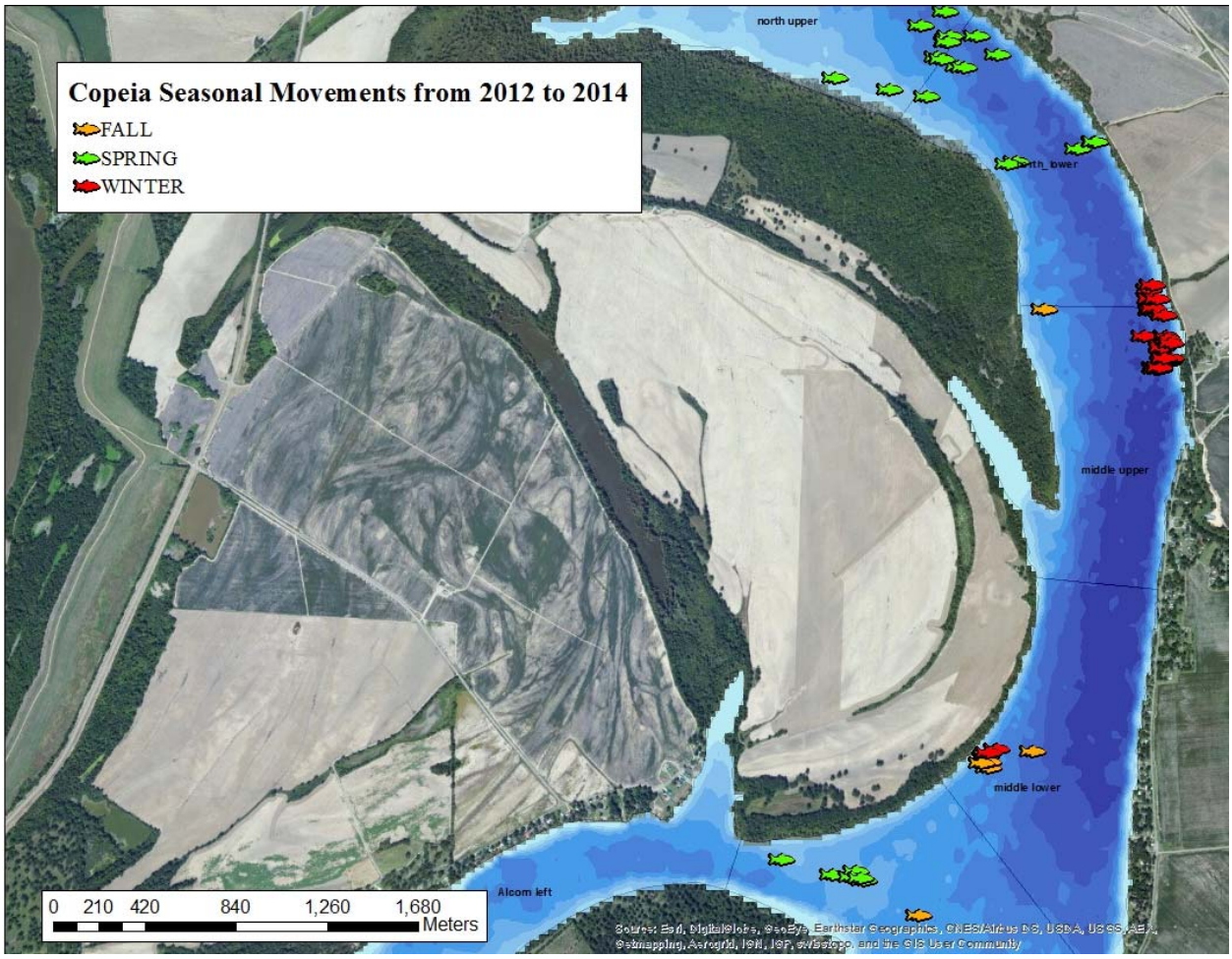

Figure 28. Seasonal movements of *Copeia* from 2012 to 2013

daylight hours with few locations observed during crepuscular periods (Figure 29). Only a single location was recorded during the night. *Copeia*, a smaller paddlefish (exact size unknown), may have remained in deeper waters out of radio signal or may have ventured into backwaters or other remote locations.

Four fish were captured on March 21, 2013. The fish ranged in size from 881 to 889 millimeters eye-to-fork length and had rostra ranging in size from 448 to 508 millimeters. All paddlefish were relatively robust with condition factors ranging from 1.79 to 2.22 (Table 21). The four fish were named after the Greek water gods, *Aegaeon, Akheilos, Amphitrite,* and *Anapos.*

Aegaeon was captured at 34.43085°N latitude and -90.49955°W longitude. This paddlefish was located a total of nineteen times over the span of 16 days (Figure 30). The paddlefish was last located on April 6, 2013 and showed a disparity between daily and nightly movements. Daily movements were limited to the steep banks along the deepest ridges of the eastern shoreline (Table 22). The longest distance *Aegaeon* covered on a given day was on April 1, 2013, when the distance spanned 2.6 kilometers over an interval of three hours, forty minutes, and nineteen seconds (3:40:19). The average calculated velocity was 29.03 centimeters per second.

Akheilos was captured at 34.43525°N latitude and -90.49894°W longitude. It had an eye-to-fork length of 889 mm with a rostrum length of 478 mm. The paddlefish weighed 12.56 kg and had a calculated condition factor of 1.79 (Table 21). *Akheilos* was captured and released near 34.43525°N latitude and -90.49894°W longitude and was first located nearly 2.39 km north of its release location. The paddlefish was located a few times in this vicinity over the next several days. The fish appeared to travel to this northern location during the evening before it returned to

Table 21. Paddlefish information and measurements

Fish Index	Fish Name	Release Date	Date of Last Location	Weight (kg)	C.F.	EFL (mm)	RL (mm)	Rostral Shape Index	Rostral Area (cm2)	Area/Mass (cm^2/kg)
69	COPEIA	11/07/2012	04/25/2013	--	--	--	--	--	--	--
65	AEGAEON	03/21/2013	04/06/2013	14.29	2.03	889	508	--	--	--
66	AKHEILOS	03/21/2013	04/06/2013	12.56	1.79	889	487	--	--	--
67	AMPHITRITE	03/21/2013	06/11/2013	15.88	2.22	894	463	--	--	--
68	ANAPOS	03/21/2013	06/21/2013	12.25	1.79	881	448	--	--	--
8	POSEIDON	01/14/2014	02/25/2014†	25.63	1.91	1103	382	1.35	309	12.06
15	LIR	01/14/2014	02/24/2014†	--	--	1203	385	--	--	--
16	CETO	01/14/2014	02/25/2014†	10.03	1.85	815	330	1.37	237.55	23.68
17	TIALOC*	01/14/2014	02/25/2014†	34.02	2.4	1124	124	1.27	482.21	14.17
18	CYMOPOLEIA	01/14/2014	02/25/2014†	19.59	1.84	1021	365	1.18	491.61	25.09
19	BRIZO	01/15/2014	02/25/2014†	15.82	2.44	865	375	1.35	301	19.03
20	GALENE	01/15/2014	02/24/2014†	19.62	1.7	1048	366	1.44	383.84	19.56
21	AHTI	01/15/2014	02/24/2014†	17.41	1.94	965	360	1.24	356.86	20.5
22	NEREUS	01/15/2014	02/25/2014†	35.01	2.39	1136	418	1.34	460	13.40
23	NEPTUNE	01/15/2014	02/24/2014†	17.46	2.39	901	362	1.25	385.17	22.06
24	ALPHEUS*	01/15/2014	02/25/2014†	26.42	2.13	1074	355	1.23	283.86	10.74
37	THOR	03/22/2014	05/19/2014	--	--	--	--	--	--	--
41	LOKI	03/23/2014	04/21/2014	--	--	--	--	--	--	--
39	HULK	03/30/2014	04/12/2014	--	--	--	--	--	--	--
38	WOLVERINE	03/30/2014	03/30/2014	--	--	--	--	--	--	--
42	ALITTLEHIGH	05/03/2014	07/21/2014	--	--	830	340	--	--	--
70	AMEDHIGH	05/03/2014	06/14/2014	--	--	1025	390	--	--	--
43	SPEEDO	05/03/2014	05/19/2014✠	--	--	970	360	--	--	--
44	SPEEDOAWOL	05/19/2014	05/19/2014	--	--	--	--	--	--	--
71	LITTLEMAN	05/19/2014	05/19/2014	--	--	740	320	--	--	--
36	BIGMAN	05/19/2014	05/19/2014	--	--	1110	370	--	--	--
45	SPEEDO2	09/01/2014	09/17/2014✝	--	--	--	--	--	--	--

* denotes damaged rostrum, † fish caught during commercial fisheries 02/24 – 02/25, 2014

✠ recaptured to retrieve speedometer, ✝speedometer detached from fish

Table 22. Waypoint information for Aegaeon in spring of 2013

Month - Day	Map ID	Time	Paddlefish ID	Lake Section	Lake Depth (m)
Mar-28	1	18:04:45	AEGAEON	North lower	--
Mar-28	2	18:11:15	AEGAEON	North lower	--
Mar-28	3	18:13:35	AEGAEON	North lower	--
Apr-01	4	19:10:16	AEGAEON	Middle upper	--
Apr-01	5	19:14:16	AEGAEON	Middle upper	--
Apr-01	6	21:54:25	AEGAEON	North upper	--
Apr-02	7	01:15:35	AEGAEON	Middle upper	--
Apr-02	8	01:16:03	AEGAEON	Middle upper	--
Apr-02	9	02:23:54	AEGAEON	Middle upper	--
Apr-02	10	03:28:10	AEGAEON	Middle upper	--
Apr-02	11	04:25:17	AEGAEON	Middle upper	--
Apr-06	12	02:17:23	AEGAEON	Middle upper	--
Apr-06	13	02:38:25	AEGAEON	Middle upper	--
Apr-06	14	04:14:32	AEGAEON	North lower	--
Apr-06	15	06:19:35	AEGAEON	Middle upper	--
Apr-06	16	06:35:25	AEGAEON	Middle lower	--
Apr-06	17	06:59:24	AEGAEON	Middle lower	--
Apr-06	18	07:31:23	AEGAEON	Middle lower	--
Apr-06	19	08:52:44	AEGAEON	Middle lower	--

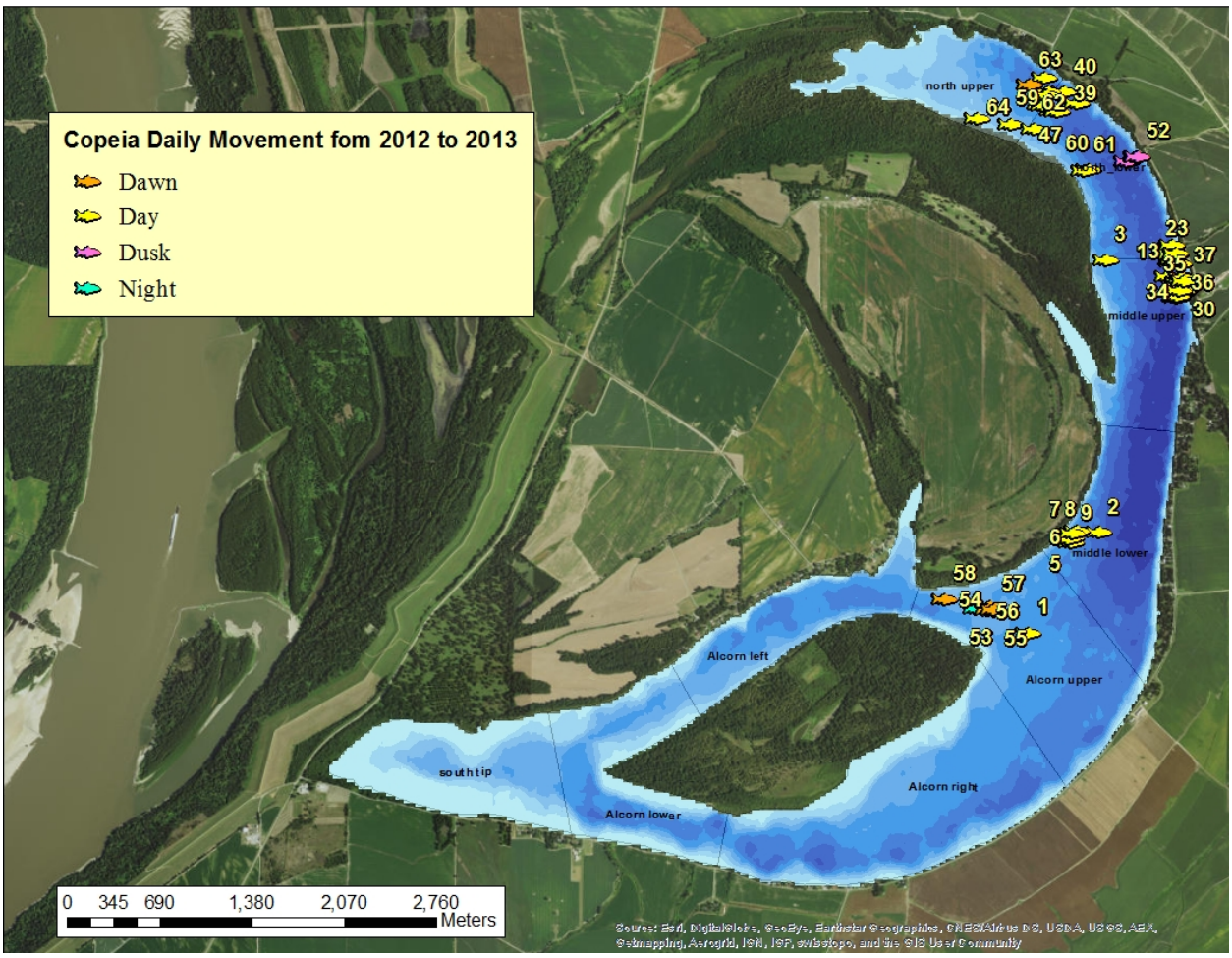

Figure 29. Daily movements of *Copeia* from 2012 to 2013

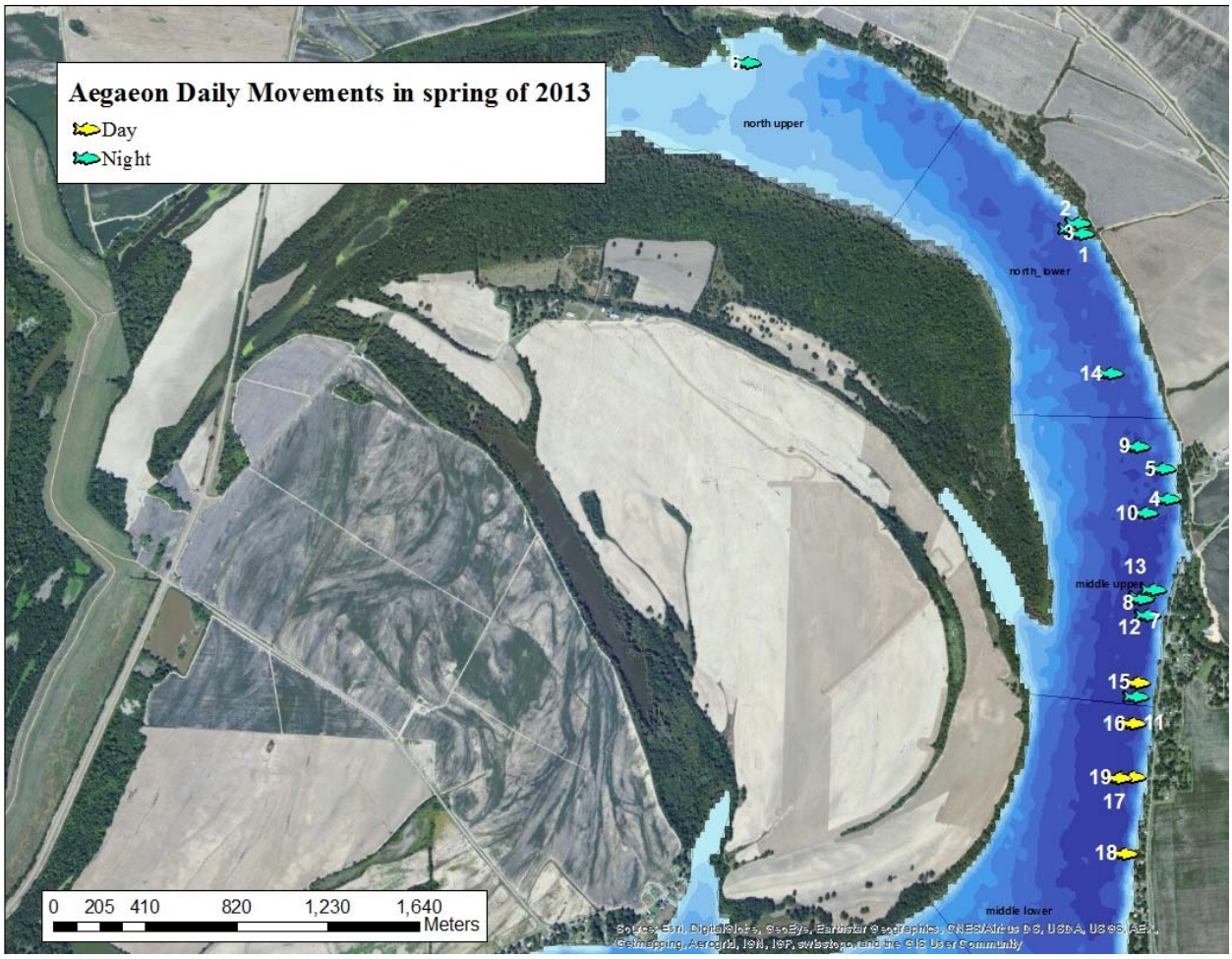

Figure 30. Daily movements of Aegaeon between March 21 and April 6, 2013

deeper waters during the day. On April 6, 2013 the paddlefish remained in deeper water for at least 11 hours (Figure 31).

Amphitrite was the most robust and active of the four paddlefish. It was caught on April 21, 2013 with a condition factor of 2.22 and a weight of 15.88 kilograms. It measured 894 mm eye-to-fork length and had a rostral length of 463 mm (Table 21). *Amphitrite* remained in the lake longer than the others, was located often (42 waypoints), and covered the widest range (Figure 32). Unlike *Aegaeon* and *Akheilos, Amphitrite* did not remain in deeper waters during daylight hours, but moved regularly into shallower sections regardless of time of day (Figure 33). The last day *Amphitrite* was located in the lake was June 21, 2013, exactly three months after it was released.

Anapos was the smallest of the fish tracked in 2013 with an eye-to-fork length of 881 mm and a rostrum length of 448 mm (Table 21). Although not as robust (condition factor 1.79; weight 12.25 kg) as *Amphitrite*, *Anapos* showed a similar range, and like *Amphitrite* remained in the lake well into the summer. The last day it was located was on June 11, 2013 (Figure 34). *Anapos* did not venture as far south as *Amphitrite*, but did venture into shallower waters regardless on diel period (Figure 35).

Paddlefish Movements in February of 2014

Tialoc

Tialoc was one of two paddlefish with a damanged rostrum (Figure 36). Tialoc was located a total of 16 separate times on eight different days (1/25, 2/1, 2/2, 2/8, 2/14, 2/15, 2/17, and 2/23) during February (Figure 37). Tialoc made a slow progression into deeper waters between January 14 to February 6. By January 25, Tialoc had moved 0.87 km southeast of its release site (Figure 37). Tialoc moved north and south along the embankment

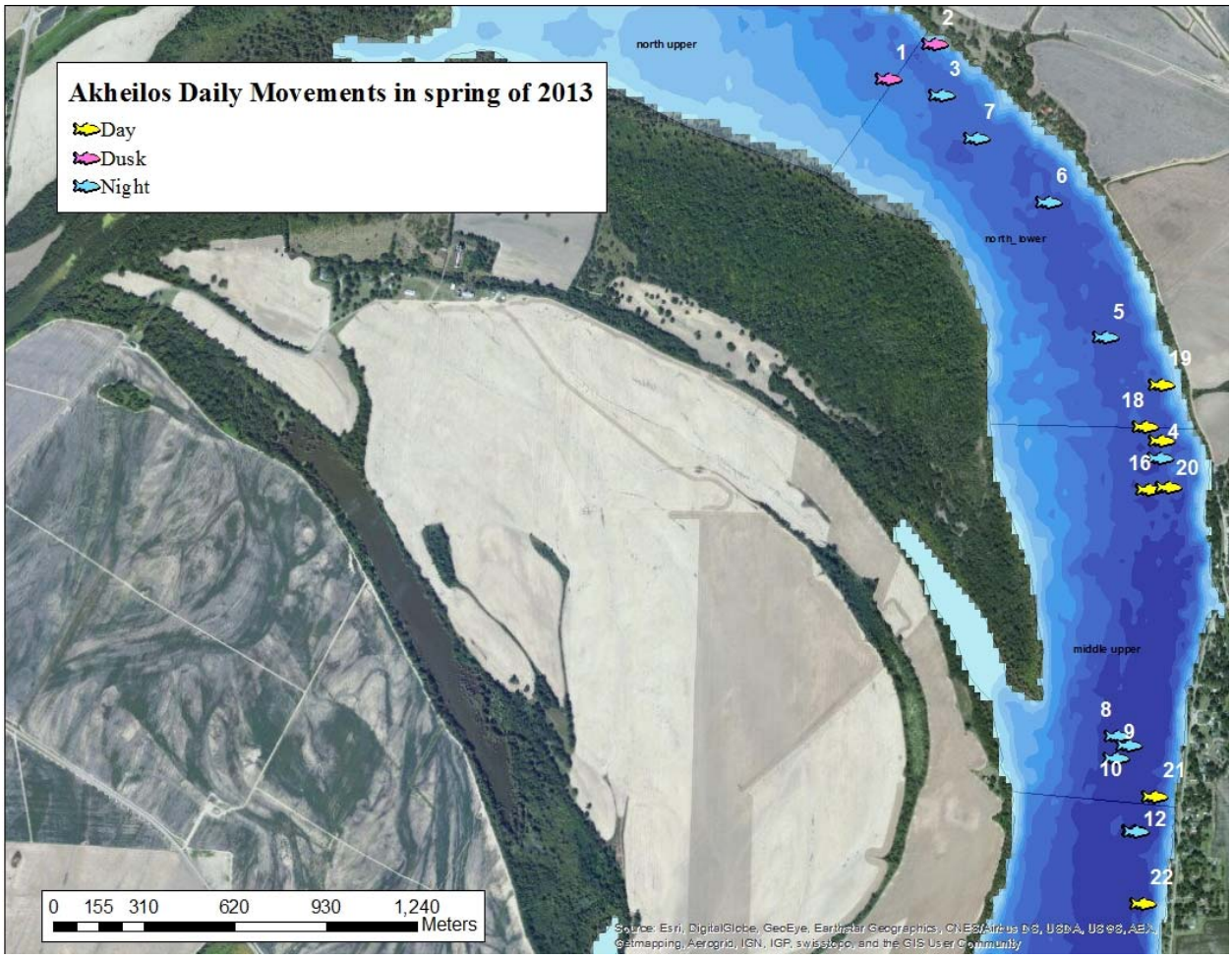

Figure 31. Daily movements of *Akheilos* between March 21 and April 6, 2013

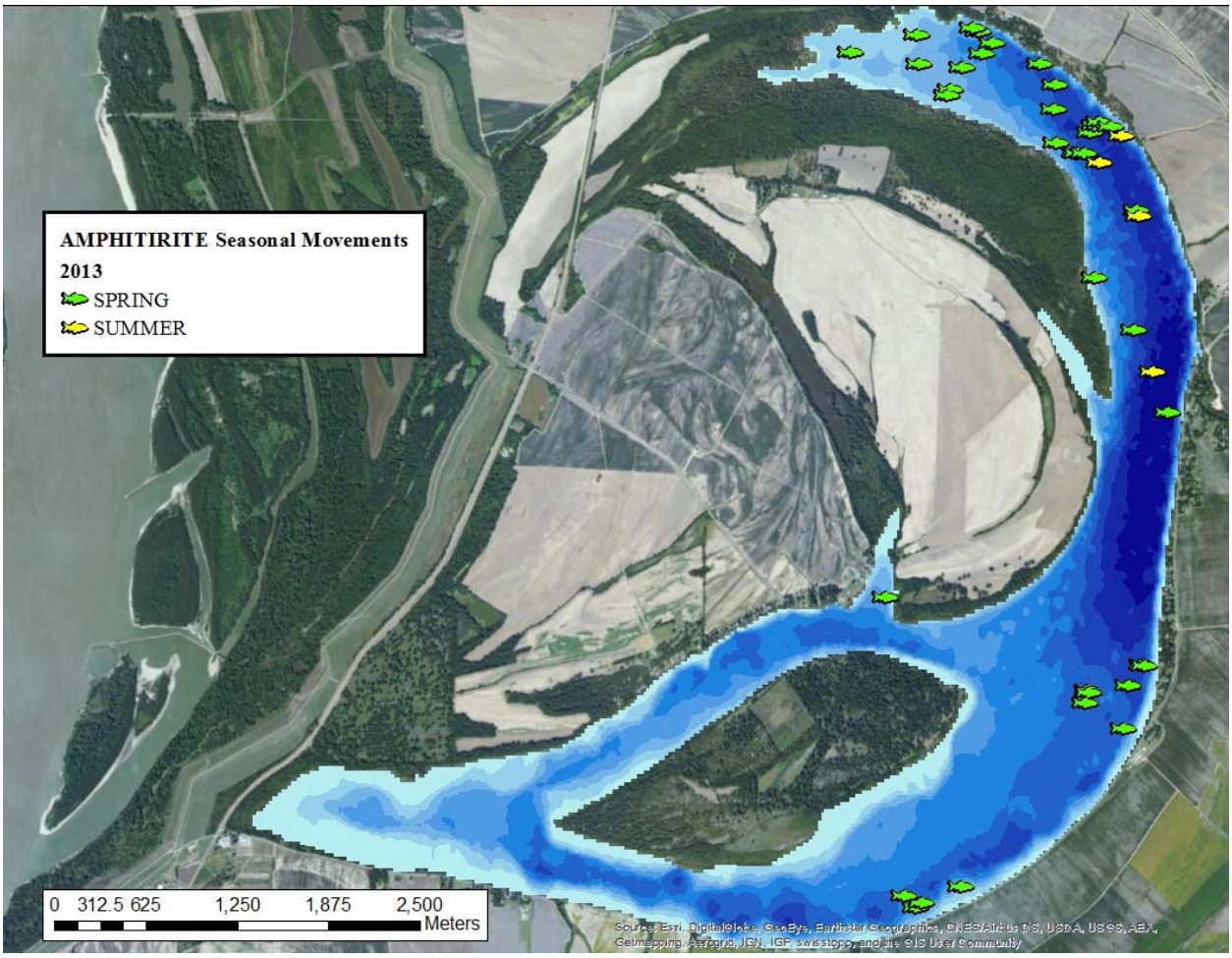

Figure 32. Seasonal movements of *Amphitrite* during 2013

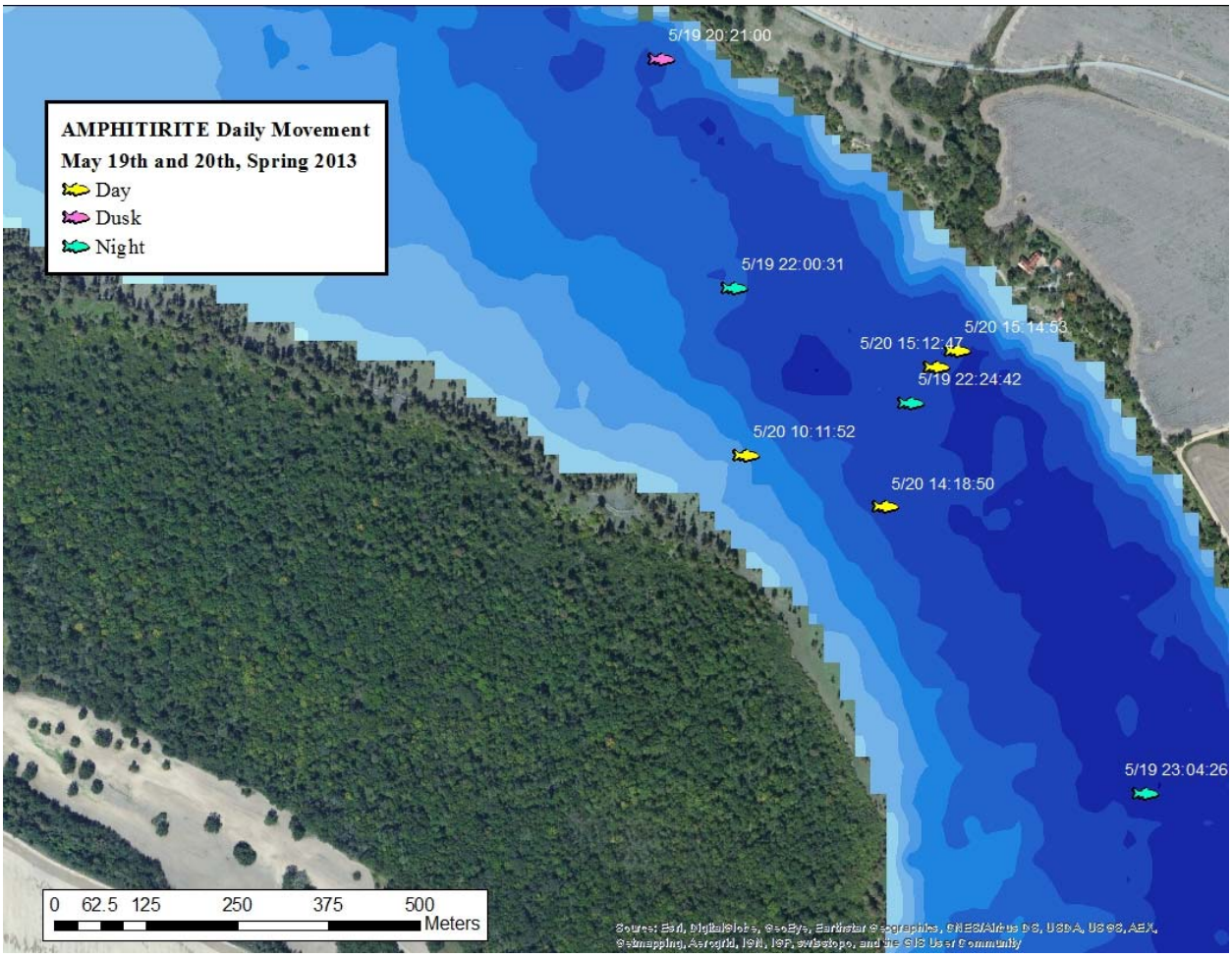

Figure 33. Daily movements of *Amphitrite* on May 19 and 20, 2013

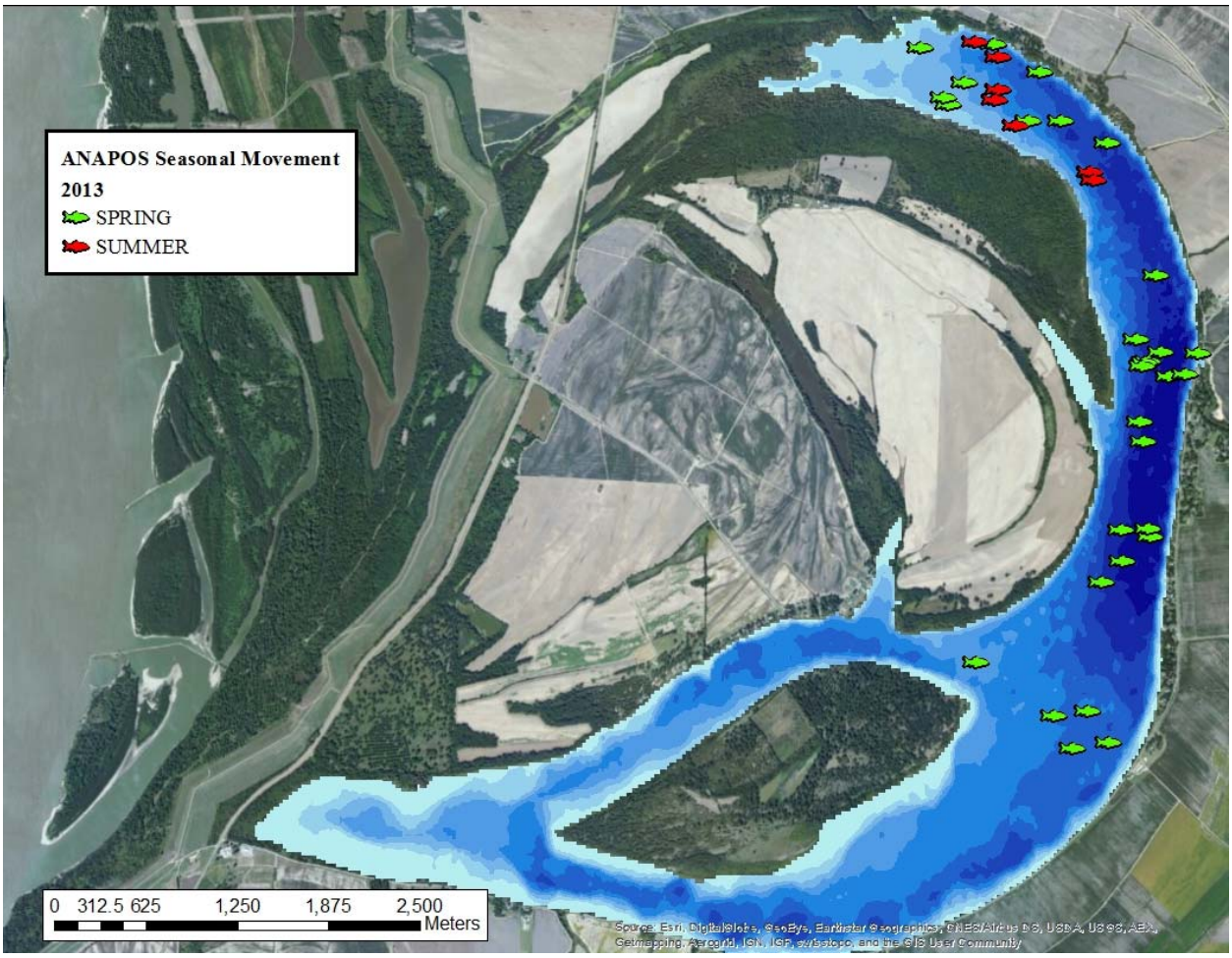

Figure 34. Seasonal movements of *Anapos* during 2013

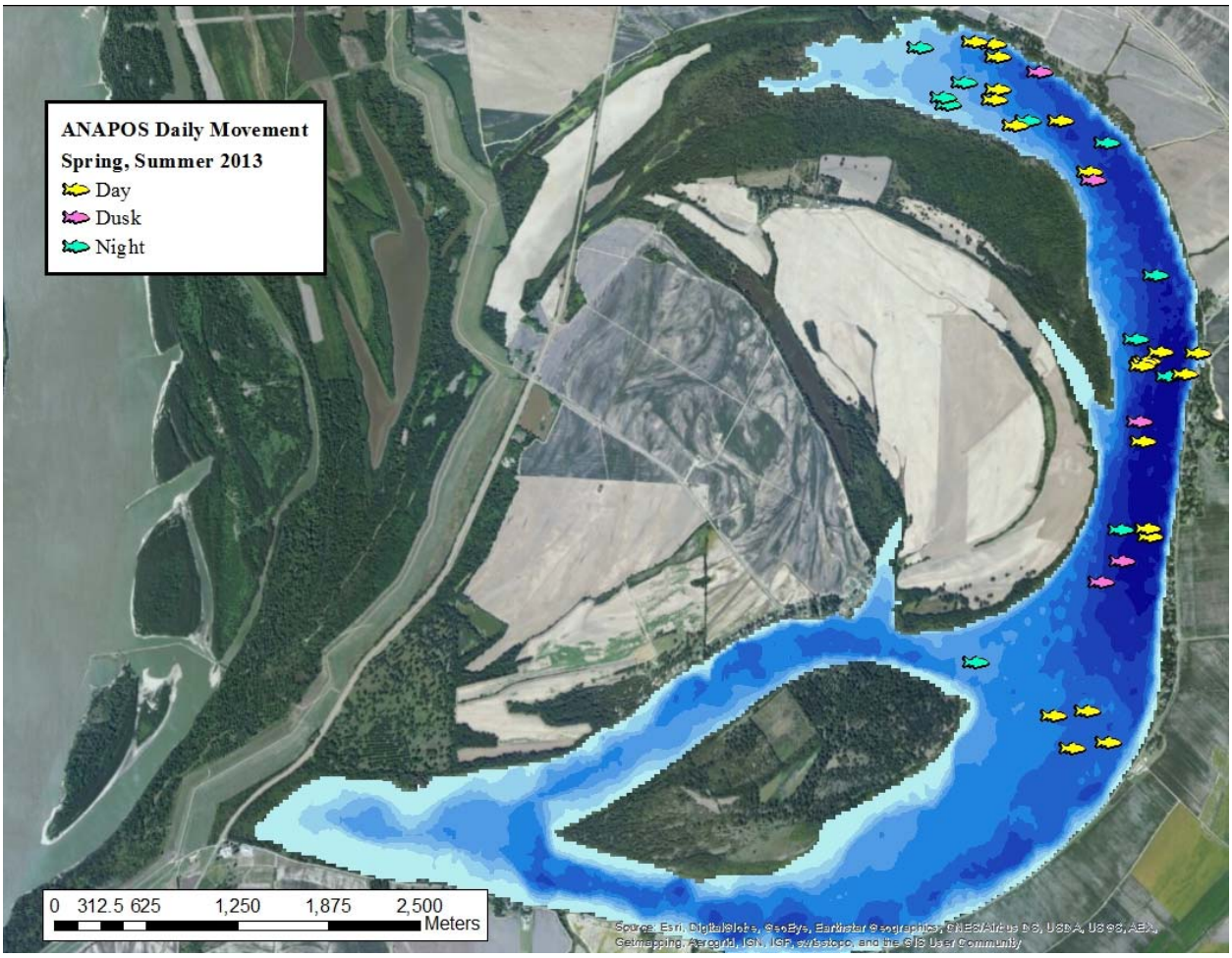

Figure 35. Daily movements of *Anapos* during 2013

Figure 36. Damaged to the Ampullae of Lorenzini on the rostrum of Tialoc

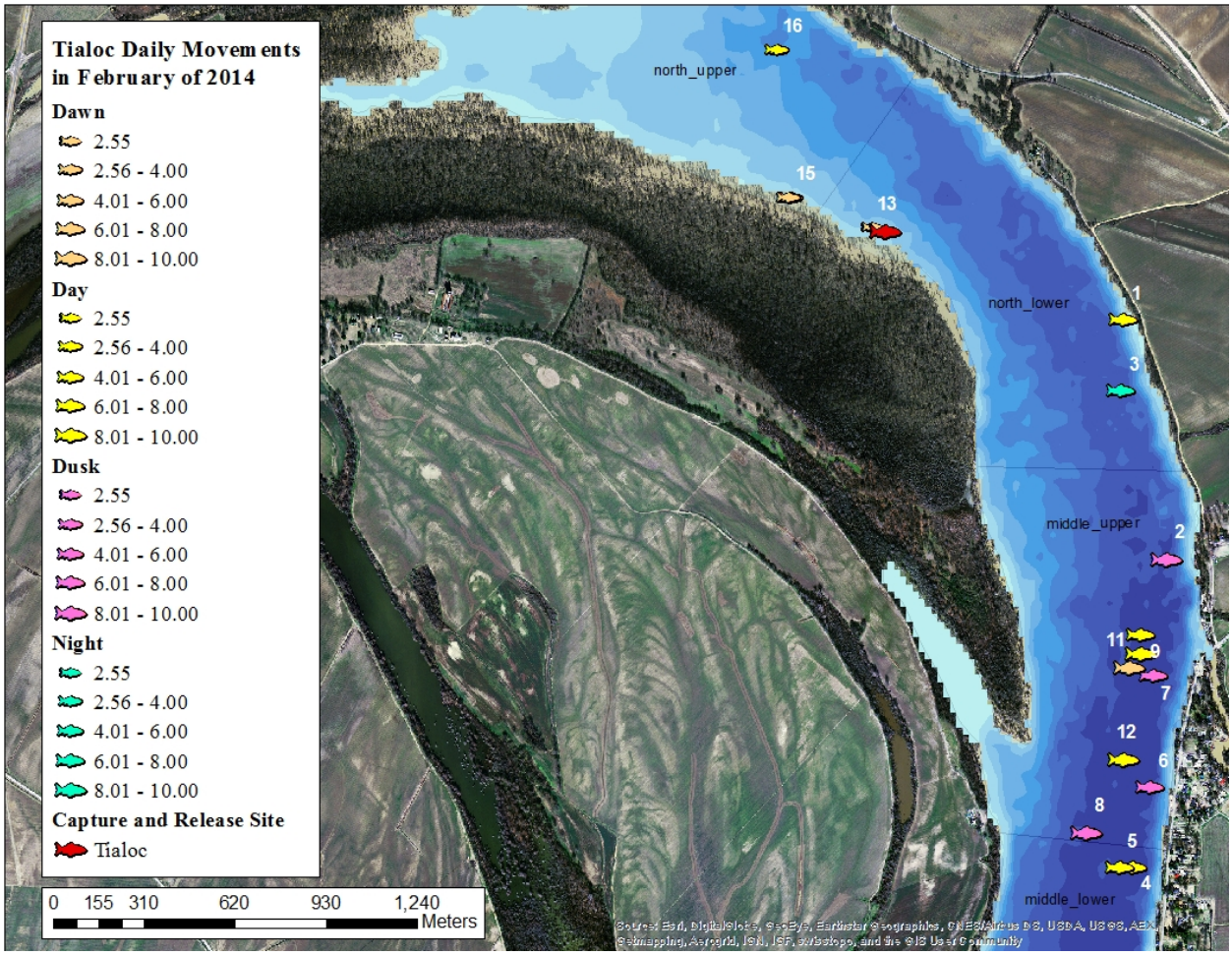

Figure 37: Daily movements of Tialoc during February, 2014

Table 23. Archival paddlefish capture and release data

Paddlefish ID	Date Released	Time Released	Date Recapture	Latitude	Longitude
AHTI	01/15/2015	15:12:00	02/24/2014	N 34.41527	W -090.50246
ALPHEUS	01/15/2015	17:35:00	02/25/2014	N 34.42239	W -090.51136
BRIZO	01/15/2015	13:55:00	02/25/2014	N 34.45199	W -090.50876
CETO	01/14/2014	12:40:00	02/25/2014	N 34.45331	W -090.50677
CYMOPOLEIA	01/14/2014	15:25:00	02/25/2014	N 34.44870	W -090.50536
GALENE	01/15/2015	15:06:00	02/24/2014	N 34.41629	W -090.50287
TIALOC	01/14/2014	13:00:00	02/25/2014	N 34.45173	W -090.50854
LIR	01/14/2014	12:22:00	02/25/2014	N 34.45270	W -090.50929
NEPTUNE	01/15/2015	16:48:00	02/24/2014	N 34.41960	W -090.51031
NEREUS	01/15/2015	16:44:00	02/25/2014	N 34.42105	W -090.51085
POSEIDON	01/14/2014	12:00:00	02/25/2014	--	--

of the eastern shoreline of the middle upper lake section between January 25 and February 1 swimming at an average depth of 2.58 meters (Figure 37: waypoints 1, 2, and 3). By February 8, Tialoc had returned south to an average depth of 7.81 meters where it remained through mid-February (Figure 37: waypoints 4 through 11). Tialoc remained in deeper waters until around February 20 before moving north into shallower waters (Figure 38). On February 23 Tialoc was found near its release location on the western shore between the borders of north upper and north lower lake sections. It traveled 0.31 kilometers northwest before moving 0.50 kilometers to the northeast. The paddlefish traveled at a velocity of 42 cm/s, swam at an average depth of 2.93 meters which was 93% of the total depth of the water column (Figure 37: waypoints 13, 15, and 16).

Ahti

Ahti weighed 17.41 kilograms and had a calculated condition factor of 1.9. The paddlefish had an eye-to-fork length of 965 mm and a rostrum length of 360. The rostrum area was 356.86 cm2 and a ratio of area to fish mass of 20.5 cm2/kg. The rostrum shape was spatulate with a rostrum shape index of 1.24 (Figure 39; Table 21). Ahti was located a total of 10 times on 4 different days (2/1, 2/15, 2/16, 2/23) in February, 2014. Ahti gradually moved from a depth of 1.75 meters on January 15 to a depth of 5 meters on January 23 (Figure 40). The average depth of occurrence was 2.85 meters and the average temperature was 5.45°C. Between January 23 and January 31 the average depth of occurrence was 4.8 meters and the fish was located in water averaging 3.3°C. The first of three waypoints was taken on February 1. Ahti was located heading north, traveling over deeper water (8.5 m), but was in the upper 20% of the water column at a depth of 1.53 m and at a temperature of 3.11°C. The paddlefish was located after 3 hours and 53 minutes at a distance of 1.6 km between

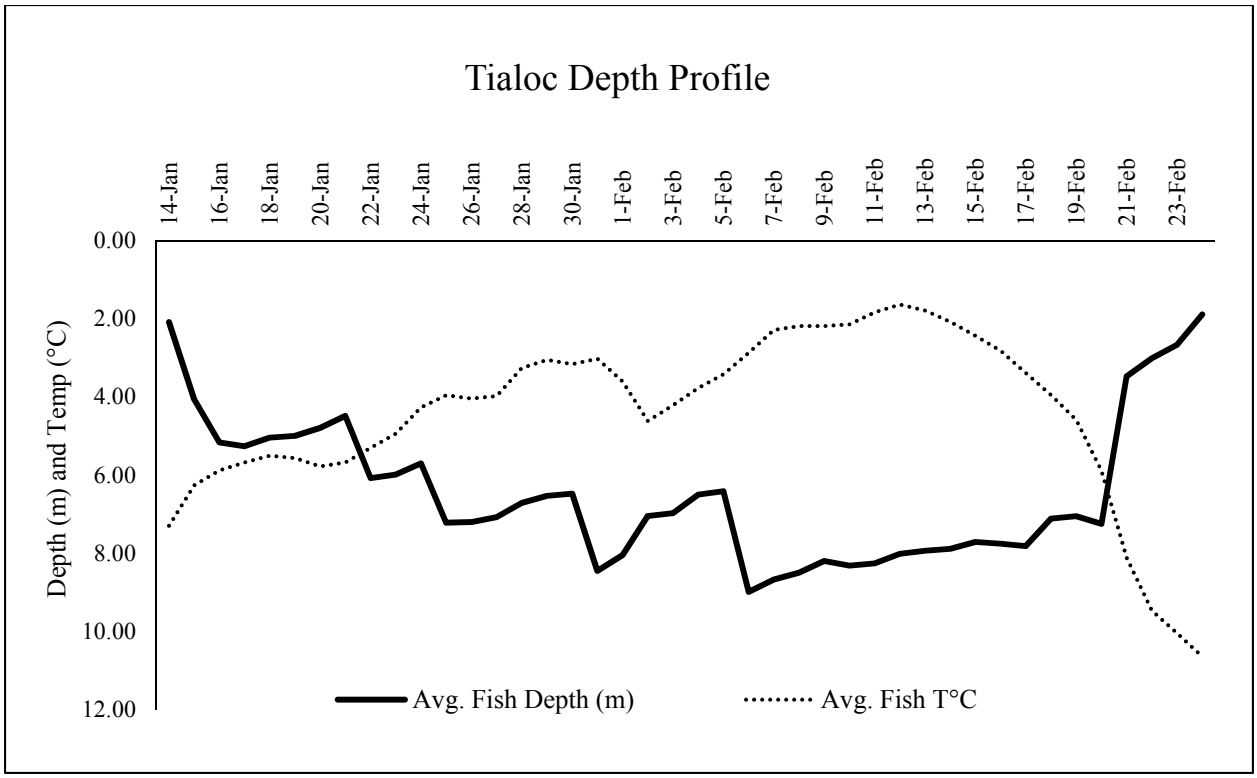

Figure 38. Average depth (m) and water temperature (°C) for Tialoc from January 15 to February 24


Figure 39. Photograph of Ahti's rostrum

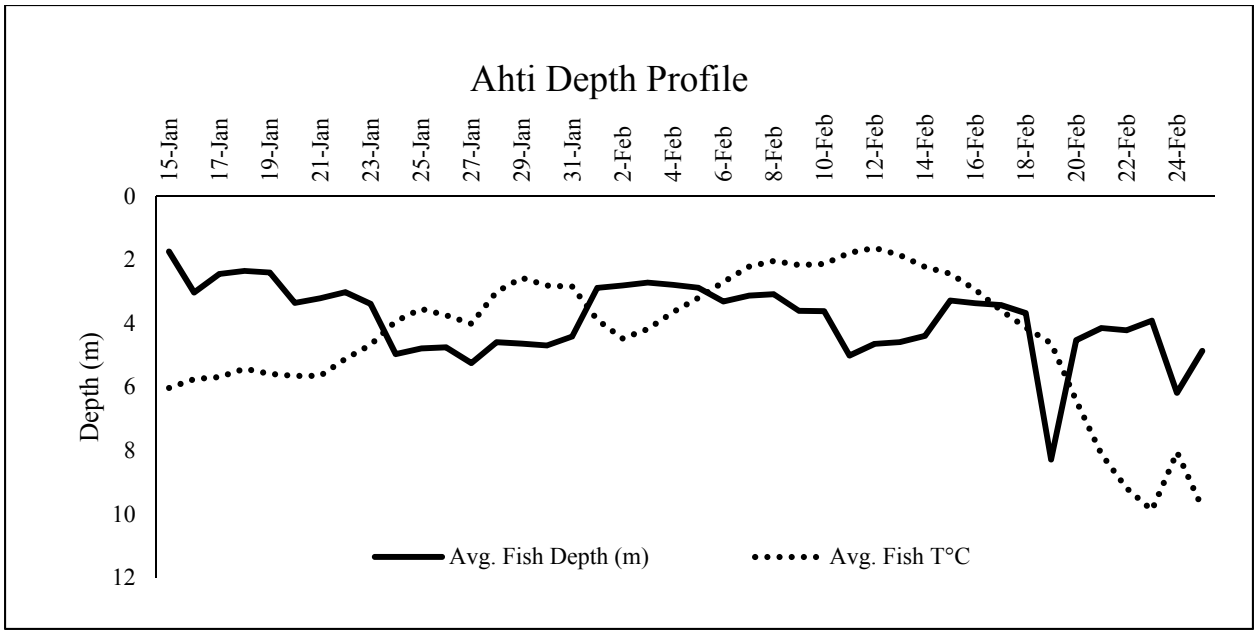

Figure 40. Average depth (m) and water temperature (°C) for Ahti from January 15 to February 24

waypoints 1 and waypoint 2. The fish was located near the shallow banks in the northwest section of the lake (Figure 41; waypoints 1 and 2). Ahti remained in this general vicinity for the next 14 and one half hours at an average depth of 2.83 meters and a temperature of 4.19°C. Ahti remained at this relatively shallow depth for the next 8 days until February 10. On February 11 Ahti descended to around 5 meters for roughly a day before coming back up on the 15th. The fish was located three times on the 15th and three times on the 16th. On the 15th Ahti moved south over two hours, covering 2.8 kilometers at an average temperature of 2.25°C, and a depth of 3.53 meters. On the 15th and 16th Ahti was located several times over a 24 hour period at the northern end of Alcorn Island at an average depth of 3.34 meters and 2.71°C (Figure 42). Ahti was highly active, traversing back and forth from the northern to southern sections. The final waypoint was recorded for Ahti at 34.45747°N latitude and -90.51203°W longitude. Tialoc was also found in this area on the same day at nearly identical times. This area is a deeper hole, nearly 5 meters deep, and was the site of a *Chaoborus* bloom.

Brizo

Brizo was one of the most robust from this group of fish with a weight 15.82 kilograms and a calculated condition of factor of 2.4 (Table 21). Eye-to-fork length was 865 mm and Brizo had a rostrum length of 375 mm. The rostrum area was 301 cm^2 and the ratio of rostrum area to fish mass was 19.03 cm^2/kg. The shape of the rostrum was spatulate with a rostrum shape index of 1.35 (Figure 43). This was among the highest in the group. Brizo was located a total of 24 times over 9 separate days. Following capture on January 17, Brizo gradually descended from 3.21 to 6.13 meters (Figure 44). From January 27 to February 7, Brizo made a couple of 2 to 3 meter vertical migrations. On February 1, 2014, Brizo was

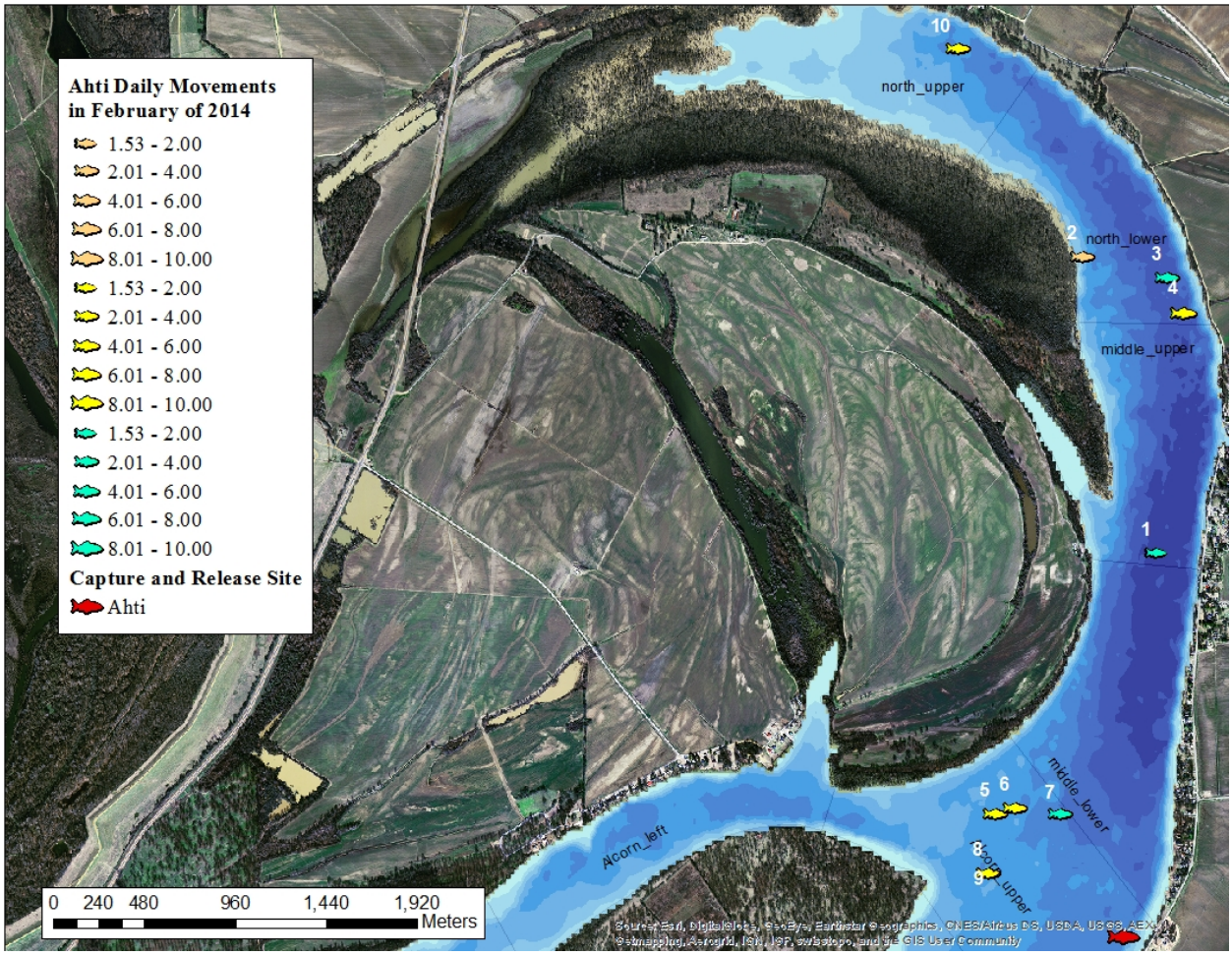

Figure 41. Daily movements of Ahti in February, 2014

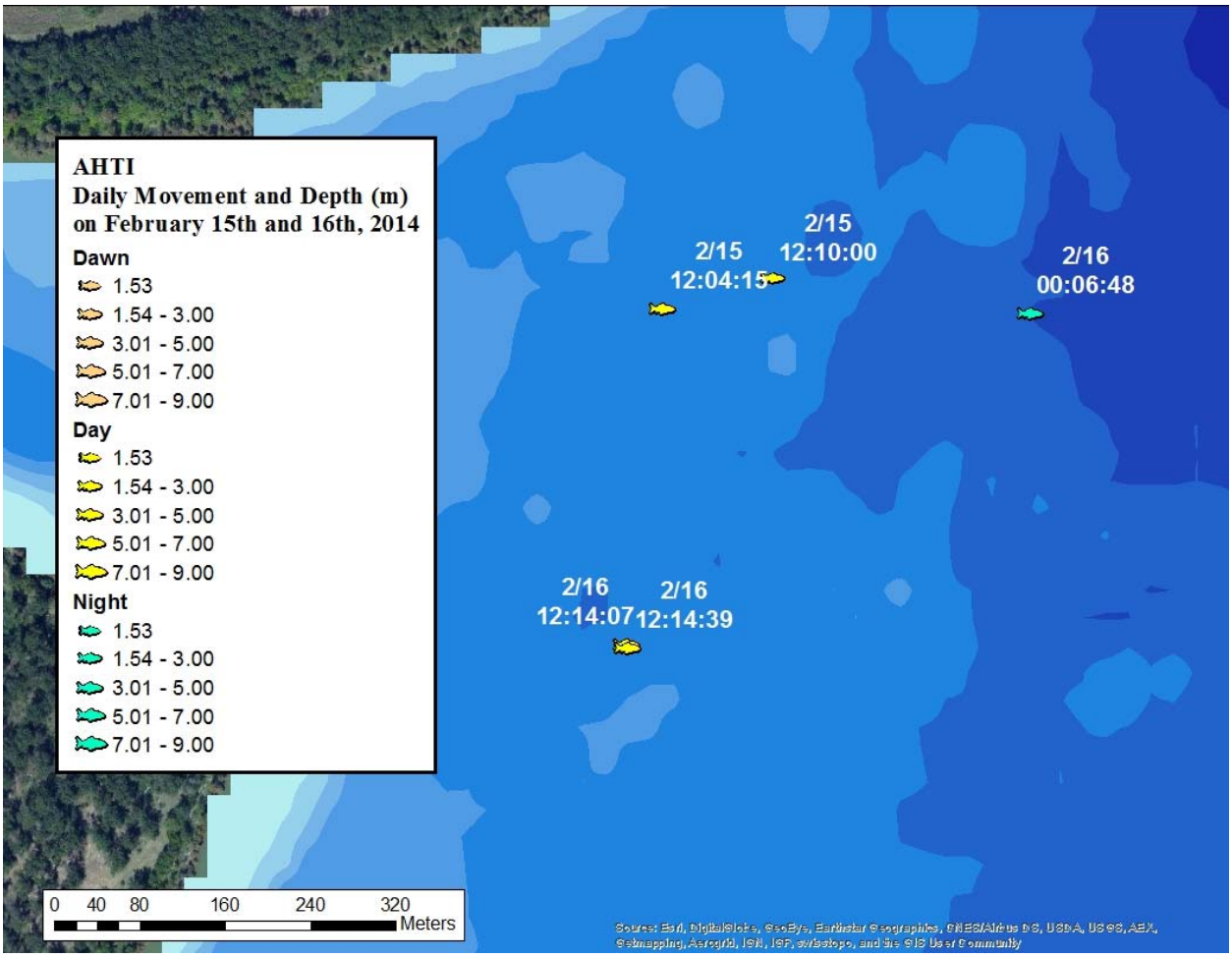

Figure 42. Daily movements of Ahti in February 15 and 16, 2014

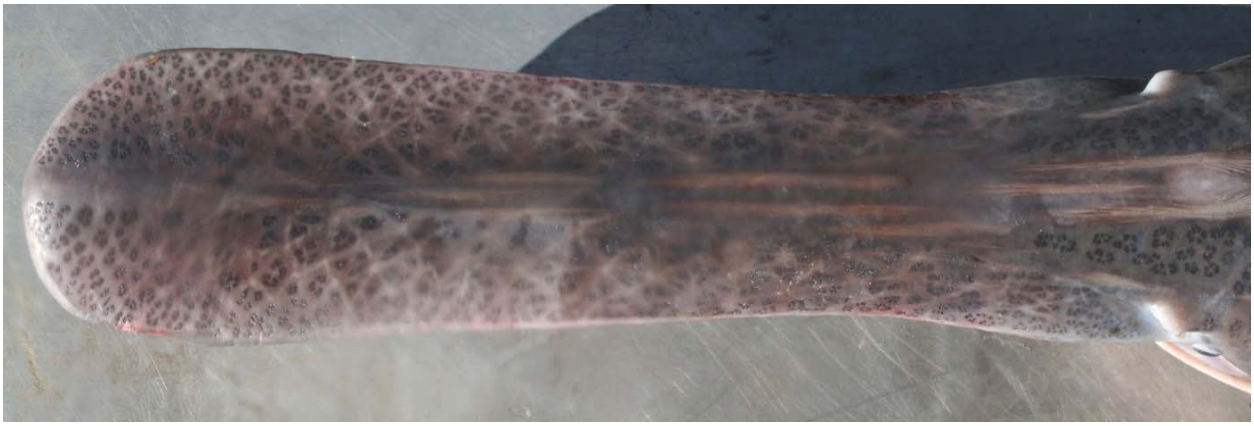

Figure 43. Photograph of Brizo's rostrum

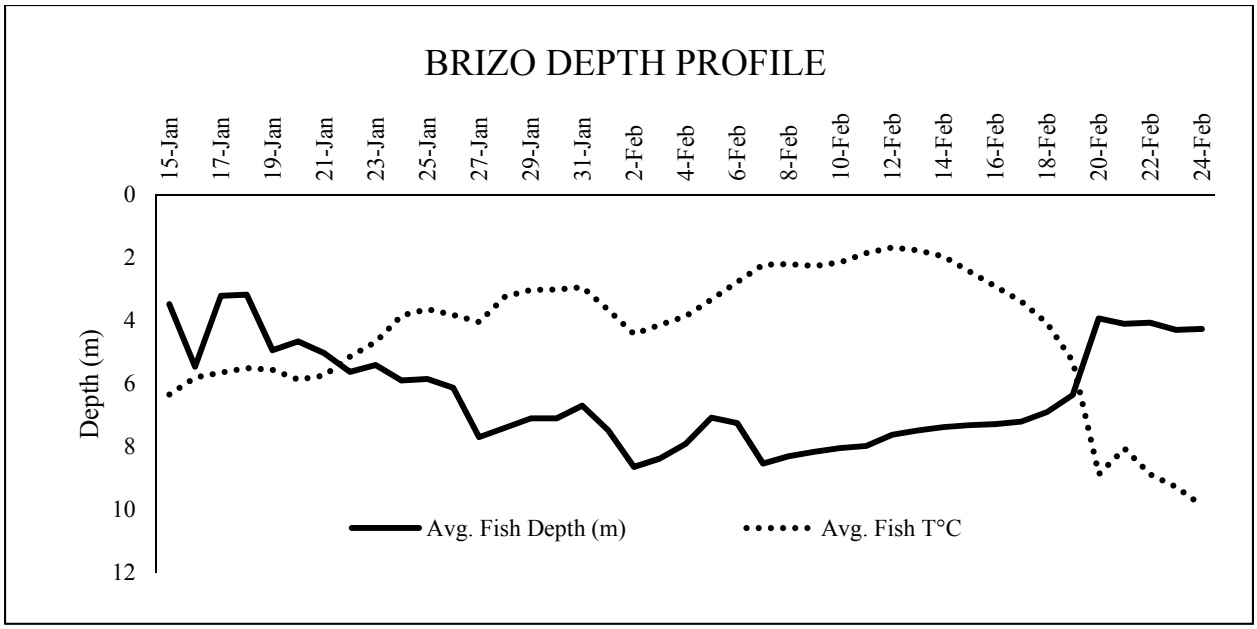

Figure 44. Average depth (m) and water temperature (°C) for Brizo from January 15 to February 24

located at 34.43148°N latitude and -90.50260°W longitude at a depth of 6.13 meters and a temperature of 6.6°C. The fish swam in the bottom 93% of the water column covering a straight-line distance of 4.69 kilometers between 7 waypoints. At dawn, Brizo was at an average depth of 7.08 meters and a temperature of 3.28°C between 0521 and 0849. Brizo remained near the bottom while it headed 1.54 km north to 34.44871°N latitude and -90.50073°W longitude traveling at an average depth of 7.54 meters and 3.54°C. By midafternoon Brizo returned to the original deeper area before leaving again at dusk. Heading due north, Brizo traveled a distance of 0.79 km at a velocity of 6.39 cm/s and returned close to its afternoon location (Figure 45).

Ceto

Ceto was the lightest of the paddlefish from this group weighing 10.03 kilograms. The calculated condition factor was 1.9 (Table 21). Eye-to-fork length was 815 mm and Brizo had a rostrum length of 330 mm. The rostrum area was 237.55 cm^2 and the ratio of rostrum area to fish mass was 23.68 cm^2/kg. The shape of the rostrum was spatulate with a rostrum shape index of 1.37 (Figure 46). Ceto was located a total of 12 times over 6 occasions and was initially located at 34.42621°N latitude and -90.50204°W longitude (Figure 47). Beginning on January 15, Ceto was at an initial depth of 7.23 meters. The paddlefish steadily ascended over 6 days peaking at 3.85 meters and a temperature of 5.84°C on January 21. Over the next 5 days Ceto gradually descended to 6.64 meters and to a temperature of 3.65°C. This was a temperature difference of more than 2°C. Ceto remained at that depth until February 4 with a brief ascension on January 30 (Figure 48). Ceto was first located on February 1 where it was swimming in the middle lower lake section at a depth of 6.12 meters and a temperature of 3.38°C (Figure 47). Two weeks transpired before a new waypoint was marked. On February 14

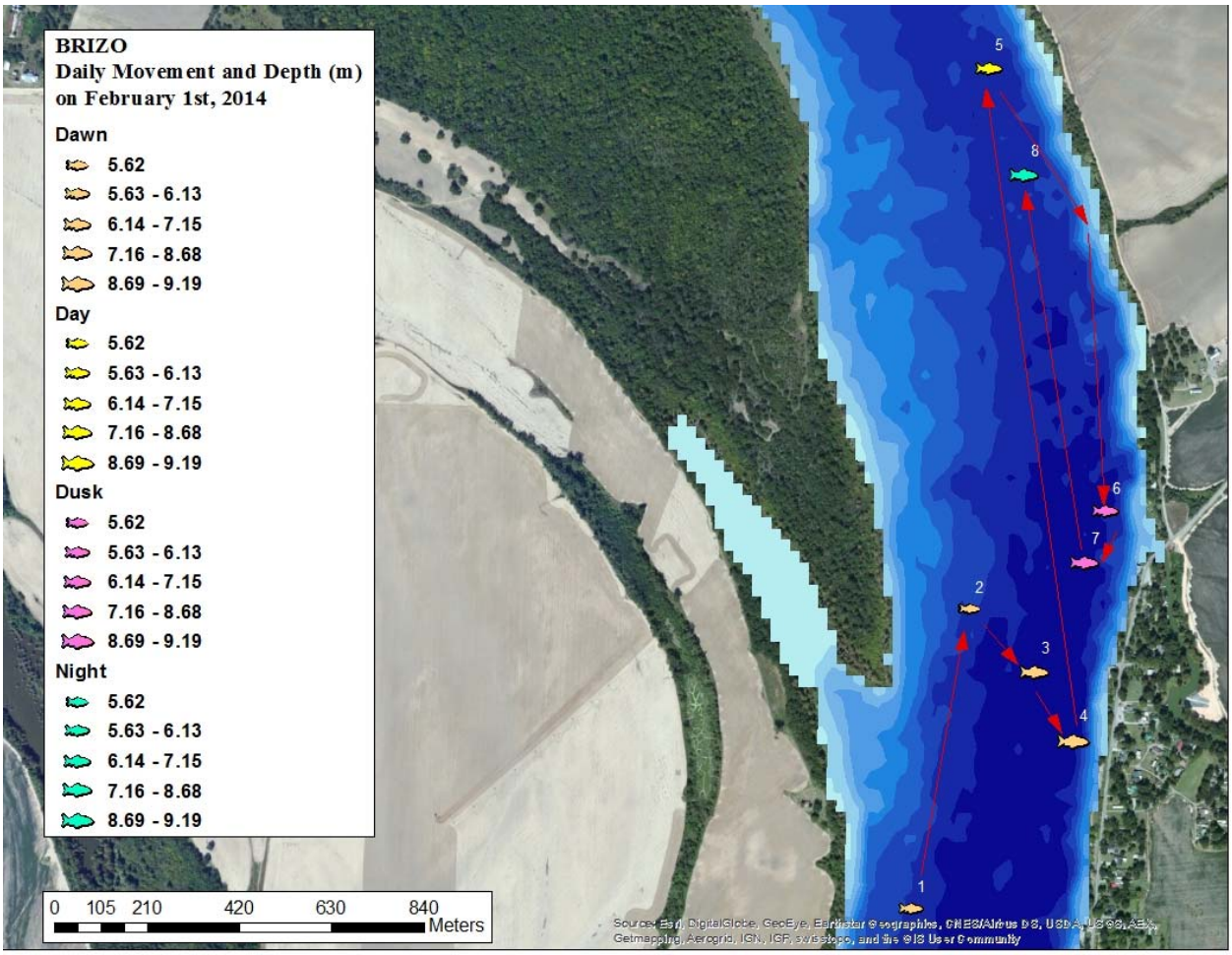

Figure 45. Daily movement of Brizo on February 1, 2014. Numbers represent depth in meters.

Figure 46. Photograph of Ceto's rostrum

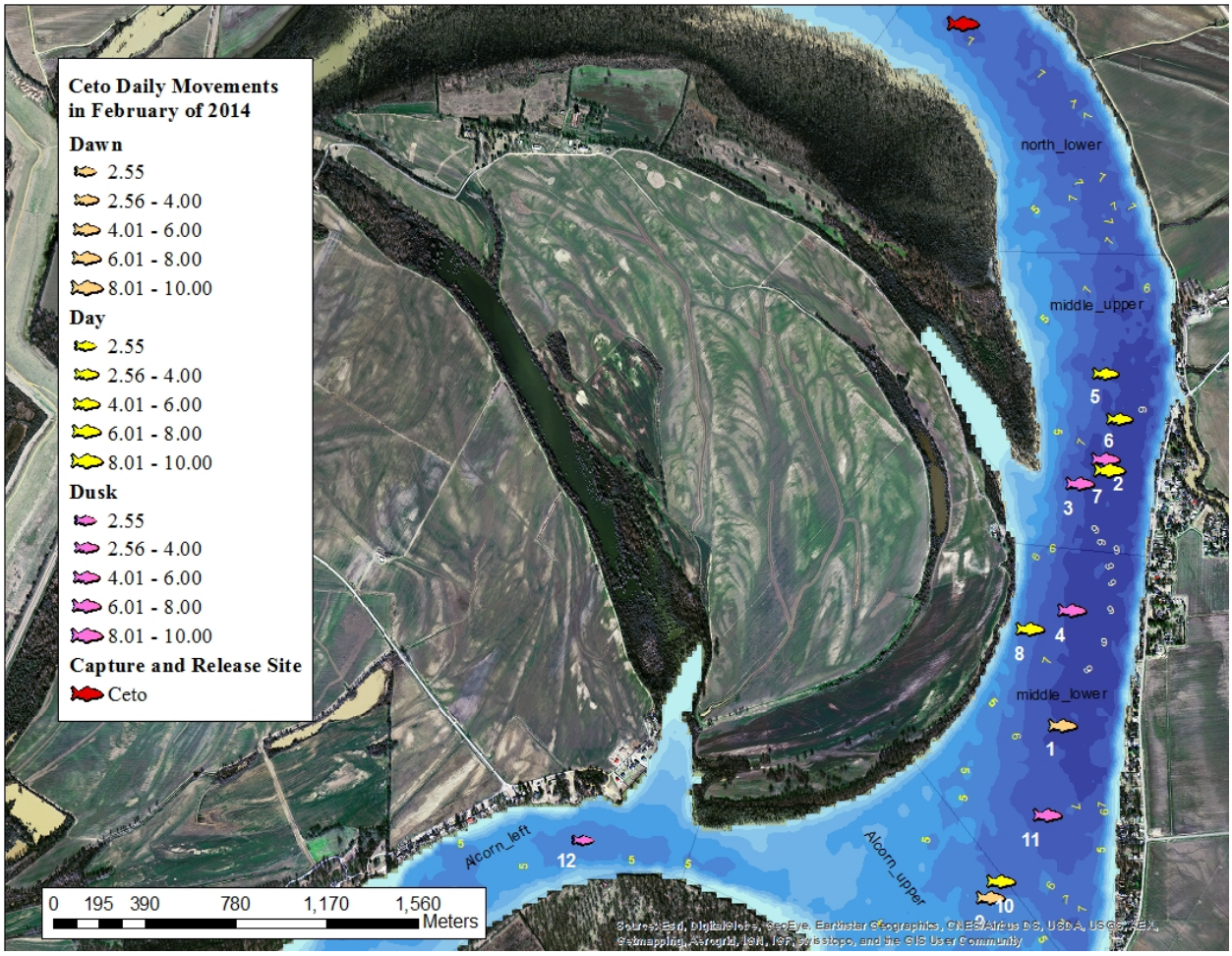

Figure 47. Daily movements of Ceto in February, 2014

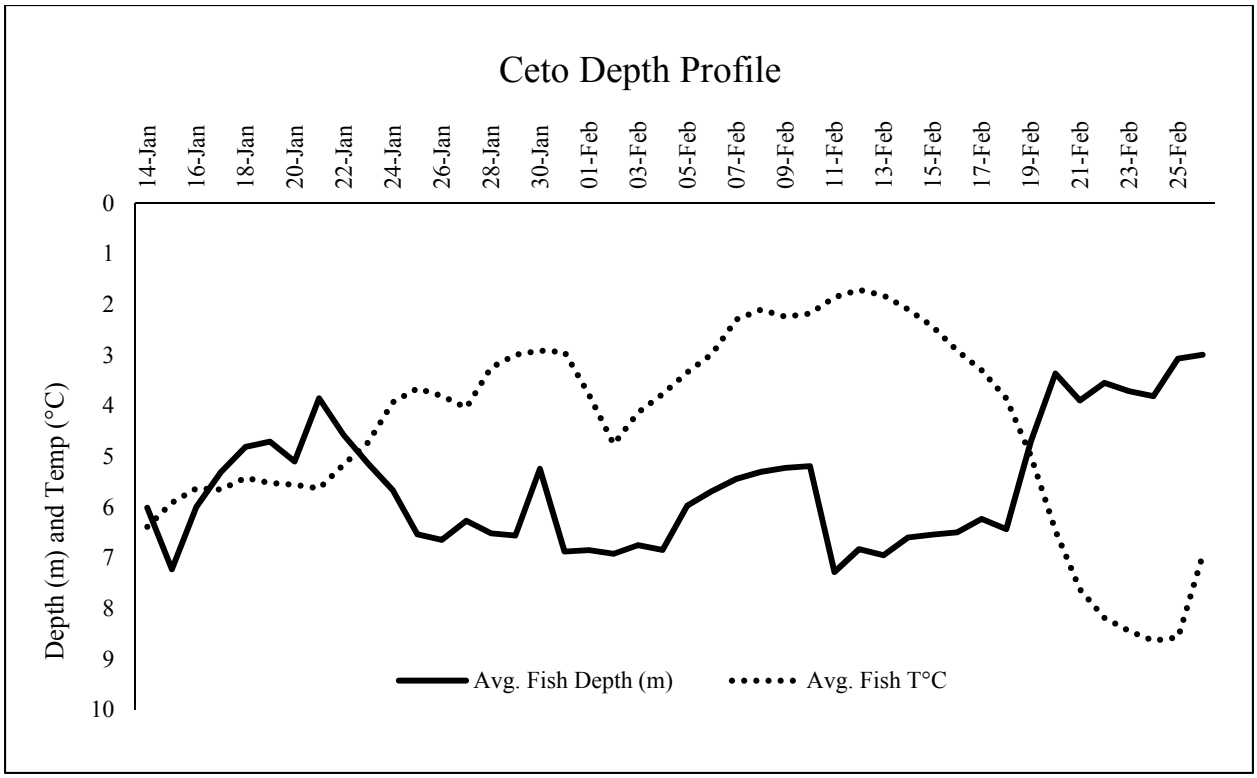

Figure 48. Average depth (m) and water temperature (°C) for Ceto from January 14 to February 25, 2014

and 15 it was located six times in the middle upper lake section swimming at 75% of the lake depth at an average of 6.52 meters and a temperature of 2.27°C (Figure 49). On January 17 Ceto spent the majority of the day between the northeast/southwest borders of Alcorn upper and middle lower (Figure 50).

Alpheus

Alpheus weighed 26.42 kilograms and had a calculated condition factor of 2.1. Eye-to-fork length was 1074 mm and rostrum length was 355 mm. Rostrum area was 283.86 cm^2 and the ratio of rostrum area to fish mass was 10.74 cm2/kg. Alpheus's rostrum had a significant portion of the upper left side removed from an apparent traumatic injury (Figure 51). The missing tissue represented approximately 7% of the original area. The original rostrum shape was slightly spatulate with a rostrum shape index of 1.23 (Table 21). Alpheus was released just northeast of Alcorn Island (Alcorn upper) on January 15 at 1635 (Figure 52). Alpheus was located 10 times over 5 days (1/25, 2/1, 2/14, 2/17, 2/23). It was located approximately one kilometer due east of its release site on January 25. Strong westerly winds of 5.9 meters per second may have influenced Alpheus's location. Most waypoints were in the middle upper section in deep water. Alpheus was located in this area on February 1, 14, and 17. On February 23 Alpheus was located in the north part of the lake at 0819 hr. Ahti, Lir, Poseidon, and Tialoc were found at a similar time in an area slightly to the north within a dense concentration of zooplankton (Figure 52: waypoints 9 and 10; Figure 53).

Cymopoleia

Cymopoleia weighed 19.59 kilograms and was 1021 mm eye-to-fork length. It had a condition factor of 1.84 and the rostrum length was 365 mm. The shape of the rostrum was rectangular rather than spatulate and had a rostrum shape index of 1.18 (Table 21). The

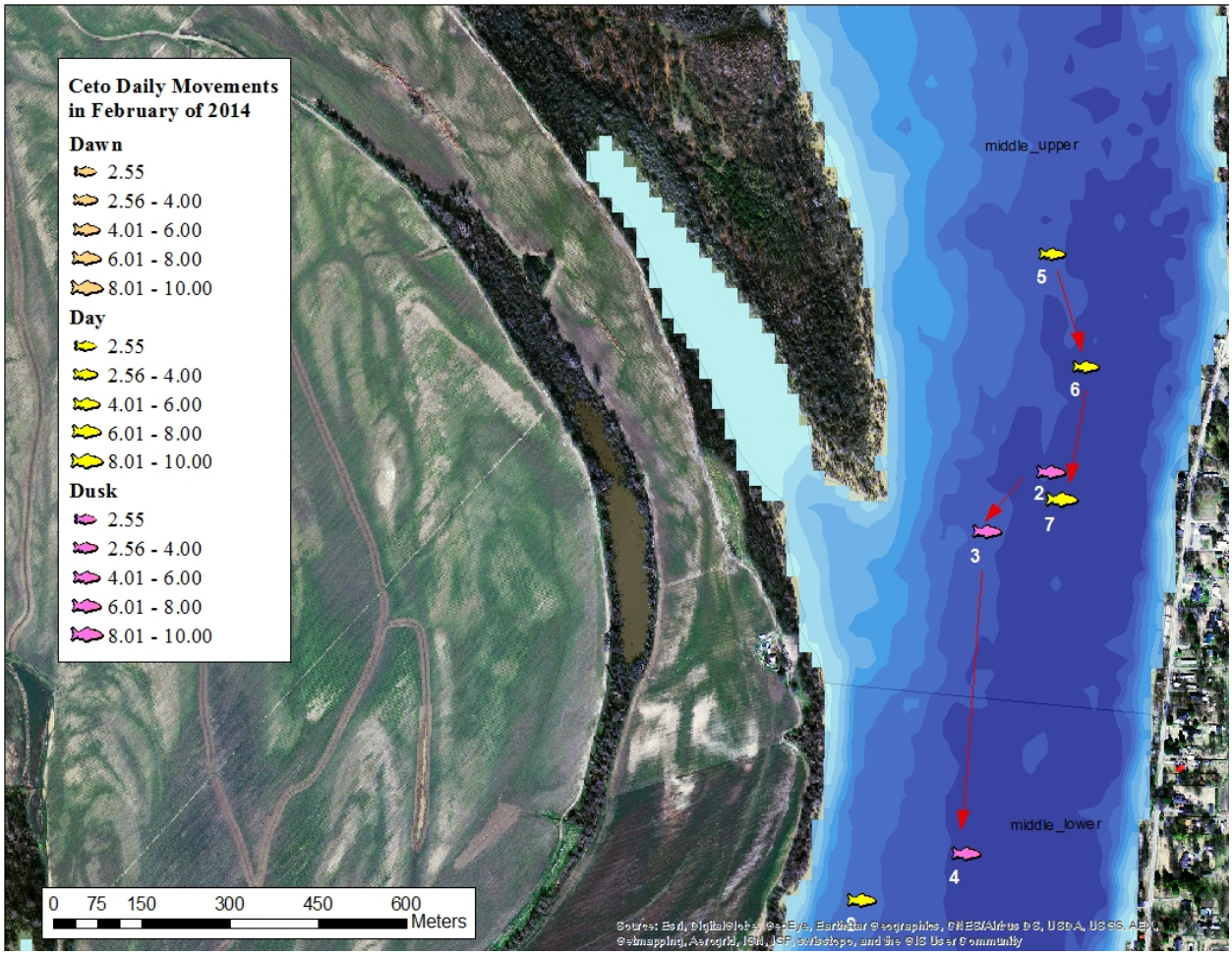

Figure 49. Daily movement of Ceto in the middle upper section of the lake on February 14 and 15

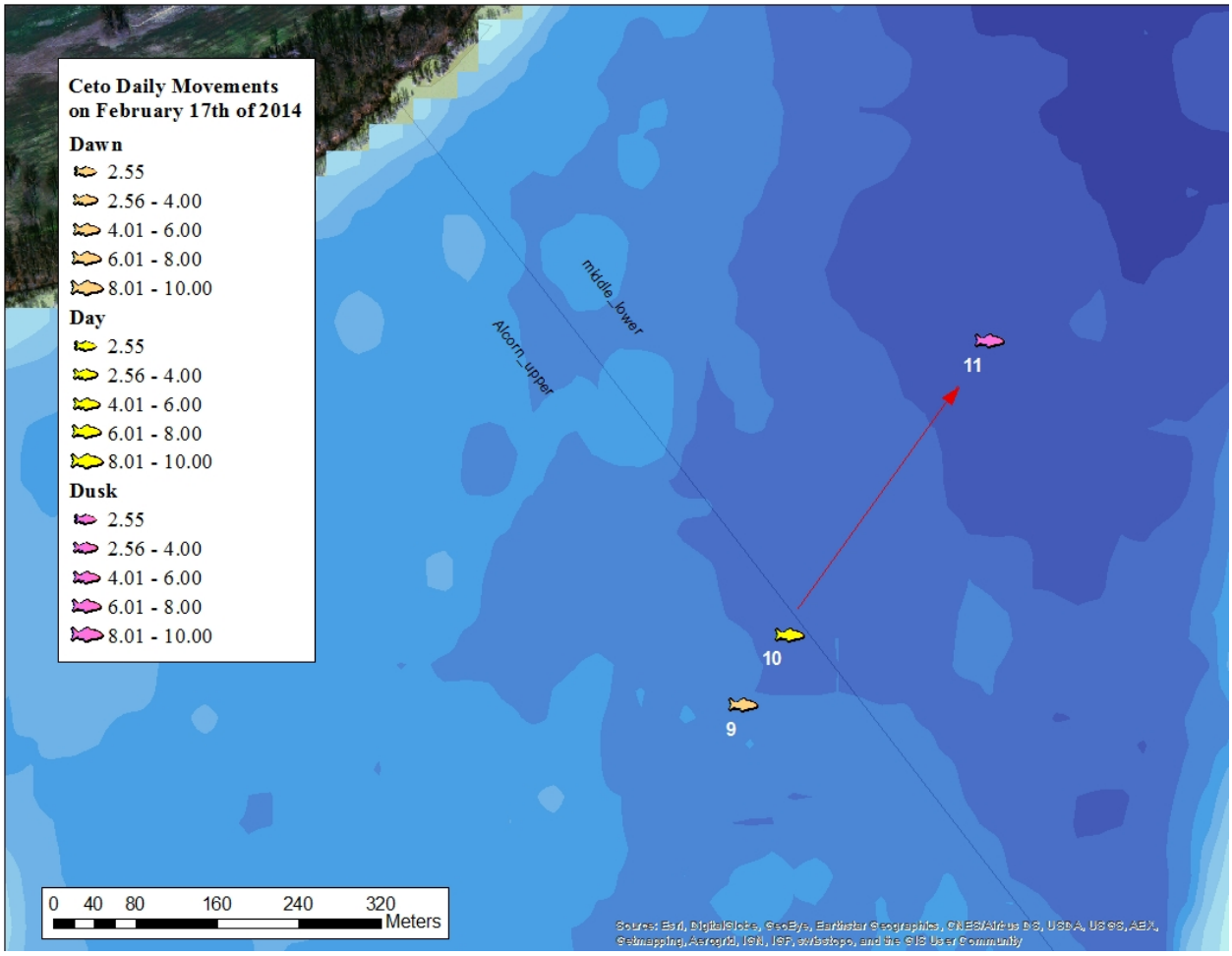

Figure 50. Movement of Ceto on February 17, 2014

Figure 51. Photograph of Alpheus's damaged rostrum

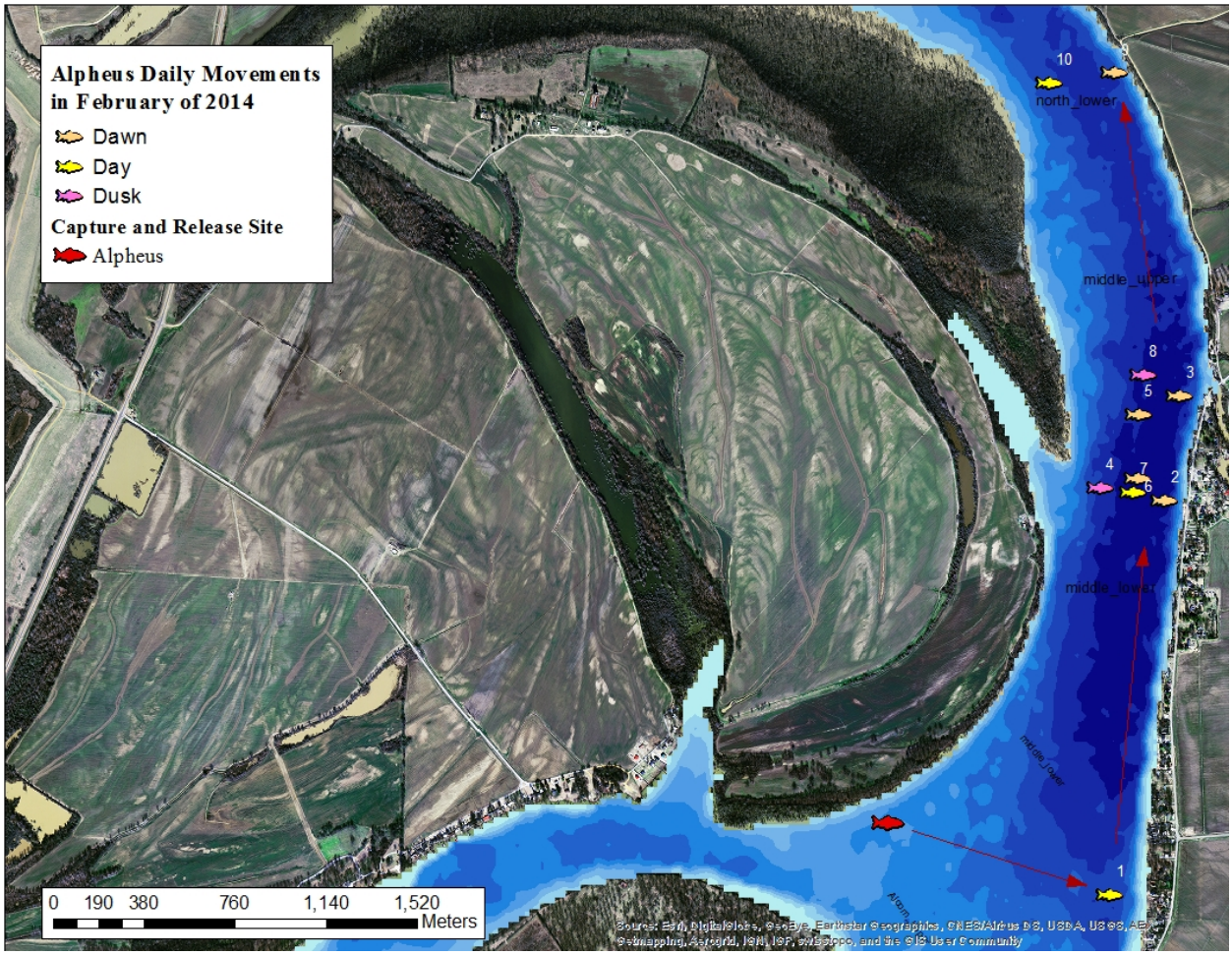

Figure 52. Daily movements of Alpheus in February, 2014

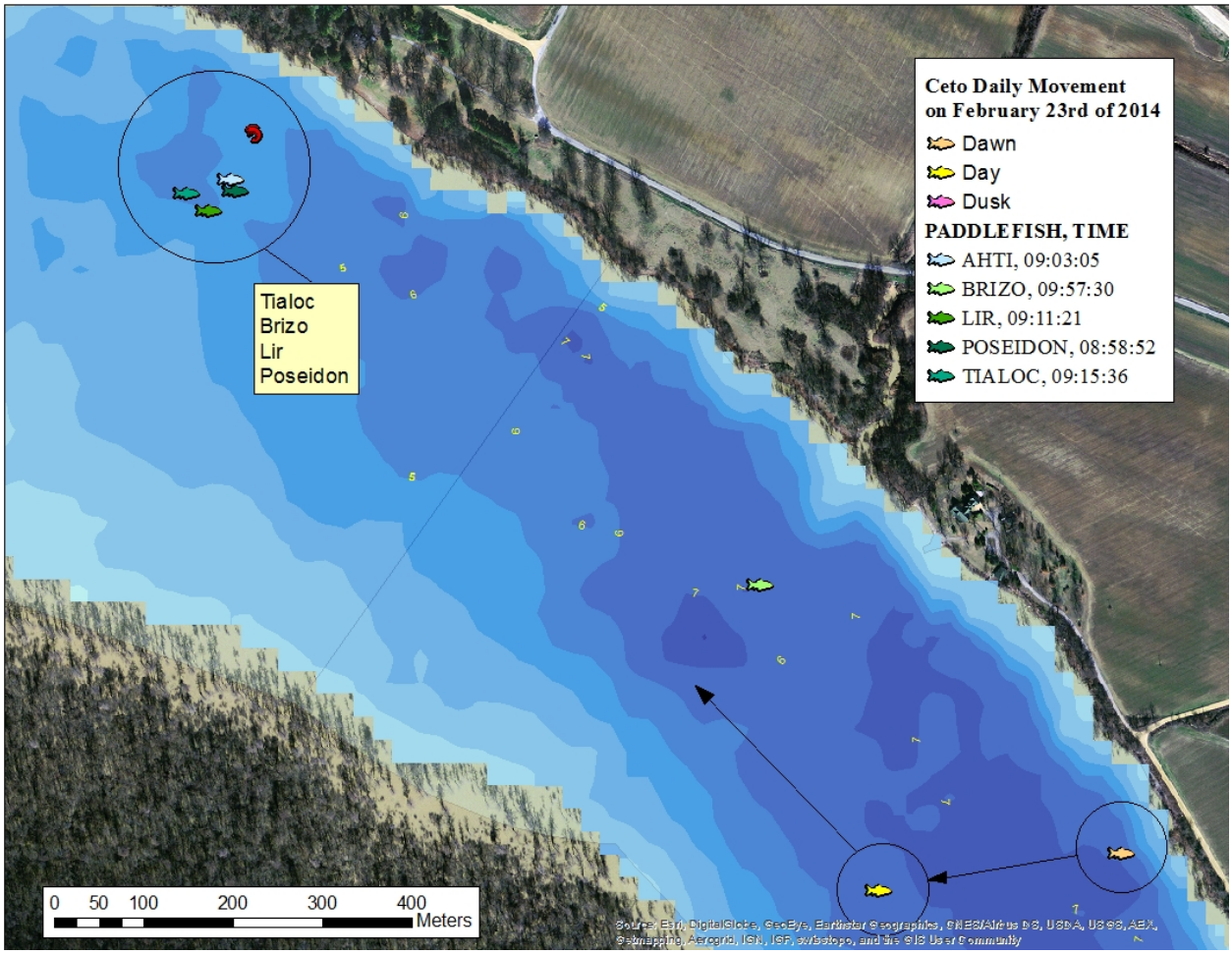

Figure 53. Movement of Alpheus on February 23

rostrum area was 491.61 cm^2 and the ratio of rostrum area to fish mass was 25.09 cm2/kg (Figure 54). Like the majority of the paddlefish in the winter, Cymopoleia spent most of its time in the deep waters of the middle upper and middle lower (Figure 55) lake sections. Twenty-four of the 26 waypoints were located in these areas. It was captured at 34.4487°N latitude and -90.50536°W longitude. It was located a total of 26 times over 8 days. The distance between its release location and the first waypoint (February 1) was a straight line distance of 1.13 kilometers. Cymopoleia was never located outside of middle upper or middle lower except on February 23 which was a day that many paddlefish were located in the north sections of the lake. The average depths of occurrence from February 2 to February 17 was 7.5 meters and the average temperature of occurrence was 2.76°C (Figure 56). Cymopoleia spent the majority of its time at depth, but on February 5 the fish ascended to above 4.5 meters, but the exact location and reason for the ascent is unknown.

Galene

Galene weighed 19.62 kilograms and was 1048 mm eye-to-fork length. It had a condition factor of 1.7 and a rostrum length of 366 mm. The shape of the rostrum was spatulate with a rostrum shape index of 1.44 (Figure 57). The rostrum area was 383.84 cm^2 and the ratio of area to fish mass was 19.56 cm^2/kg (Table 21). Galene was released in Alcorn upper lake section on January 15 and was first located in the same section 10 days later and just 0.44 kilometers to the northwest (Figure 58). Galene spent the majority of the crepuscular and nighttime periods in the deeper waters of middle upper and middle lower lake sections. It was located nine times in these two sections and usually over deeper areas. On February 2, Galene spent most of the day crossing middle lower. The paddlefish was first located in the morning around 0444 and finally crossed into middle upper in the early

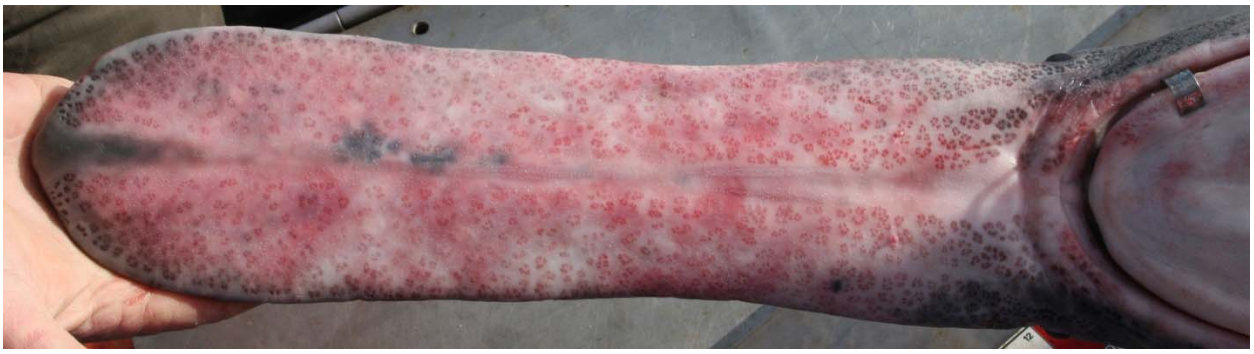

Figure 54. Photograph of Cymopoleia's rostrum

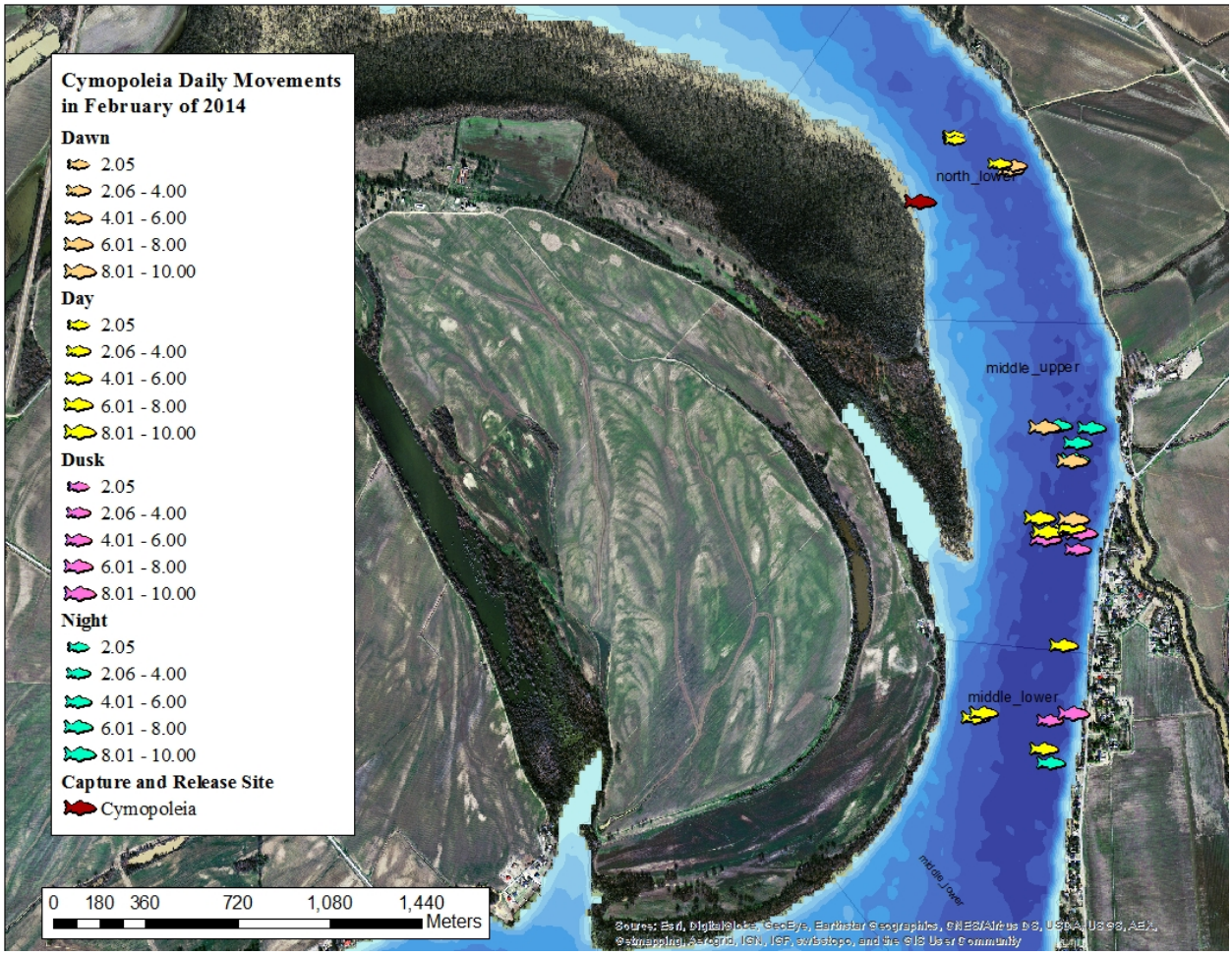

Figure 55. Daily movements of Cymopoleia in February, 2014

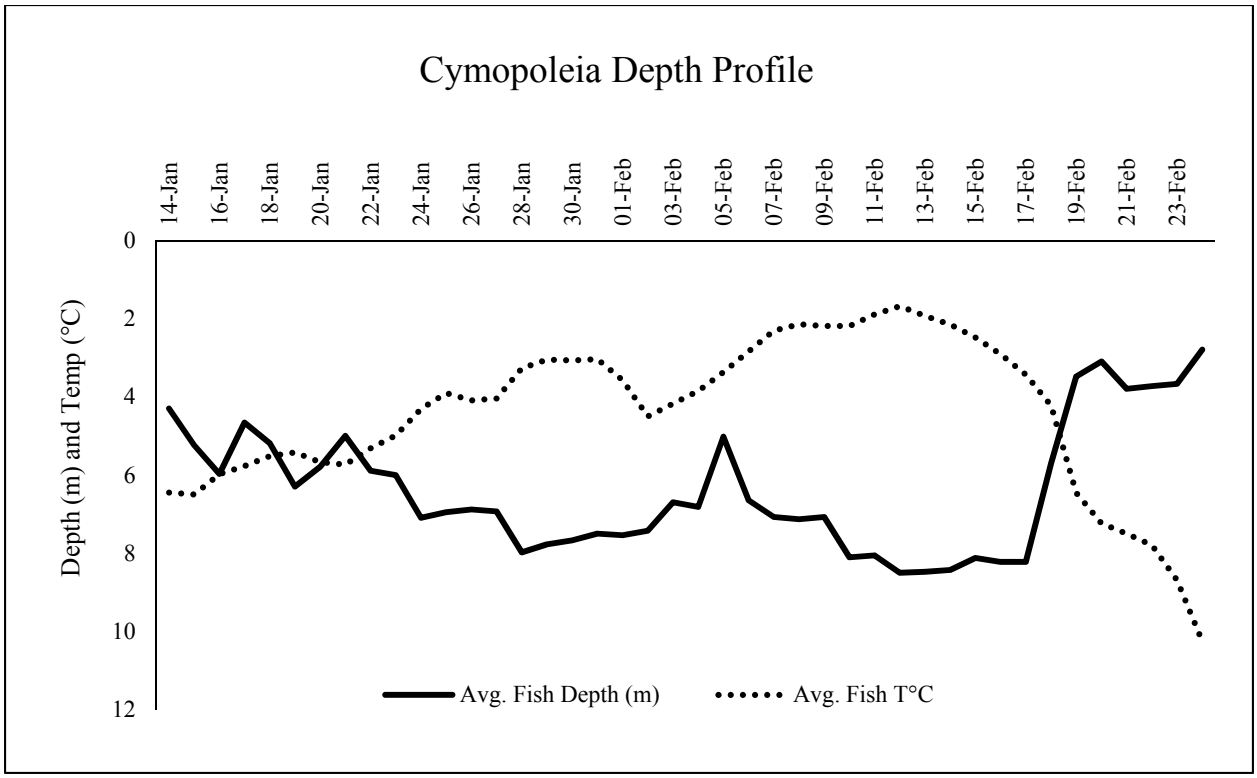

Figure 56. Average depth (m) and water temperature (°C) for Cymopoleia from January 14 to February 23

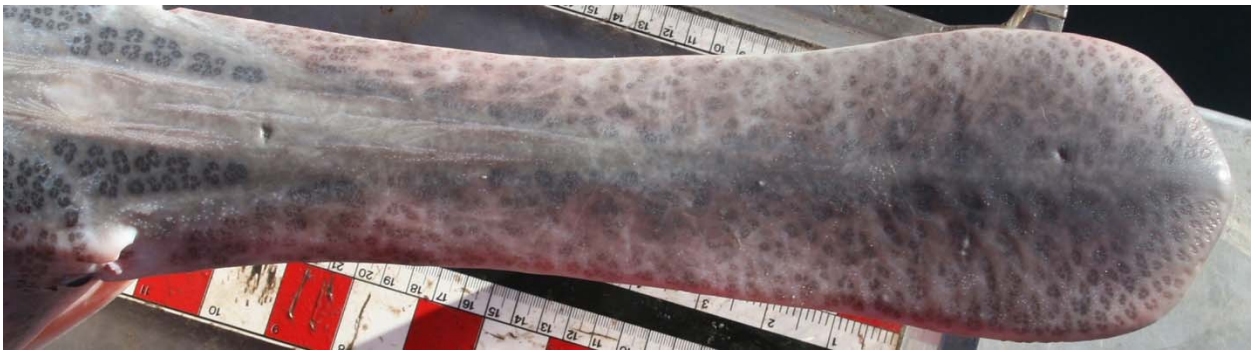

Figure 57. Photograph of Galene's rostrum

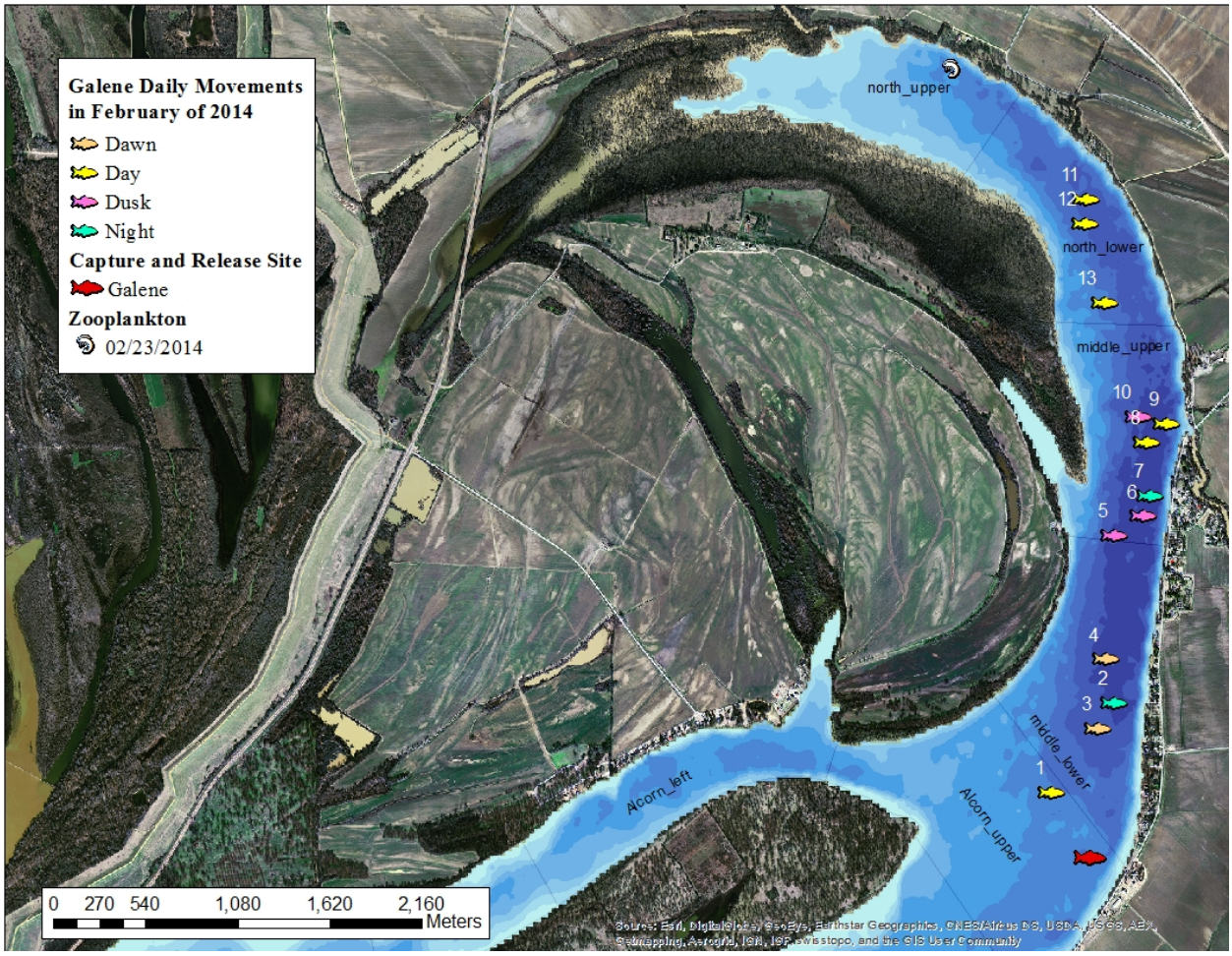

Figure 58. Galene daily movements in February, 2014

evening around 1931. It was located again seven days later only 0.20 kilometers to the northeast. It spent the next few hours within an area less than a square kilometer. Galene subsequently moved north about 0.30 kilometers, but stayed in middle upper over deep water. It's movements from midafternoon on February 15 to the early evening hours of the 16th were limited to a small area within the center of the middle upper lake section. On February 23 around 1300 hr. Galene was located at 34.45106°N latitude and -90.50317°W longitude moving in a southerly direction. Several fish had been located in the northern sections of the lake earlier the same morning on the 23. Ahti, Lir, Poseidon, and Tialoc were all found early that day in the north upper section in the vicinity of a dense patch of zooplankton (490 organisms per cubic meter). Galene may have been returning from foraging in that location.

Lir

Lir was released before its weight was taken and therefore the weight and condition factor were not measured. The rostrum area and ratio of rostrum area to fish mass could not be calculated as well. The paddlefish's eye-to-fork length was 1203 mm and it had a rostrum length of 385 mm (Table 21). Lir was released at 1222 at 34.4527°N latitude and -90.50929°W longitude on January 14, 2014. Lir descended to 5.4 meters over the next day and a half before beginning a gradual ascent to 3.5 meters over a 10 day period extending from January 16 to January 26 (Figure 59). An initial waypoint was recorded on February 1 in the southeast corner of middle lower lake section over 3.6 kilometers south from the release site (Figure 60). Lir was relatively shallow and headed north in the early morning hours. The paddlefish moved 0.65 kilometers from 0414 to 0702 at an average depth of

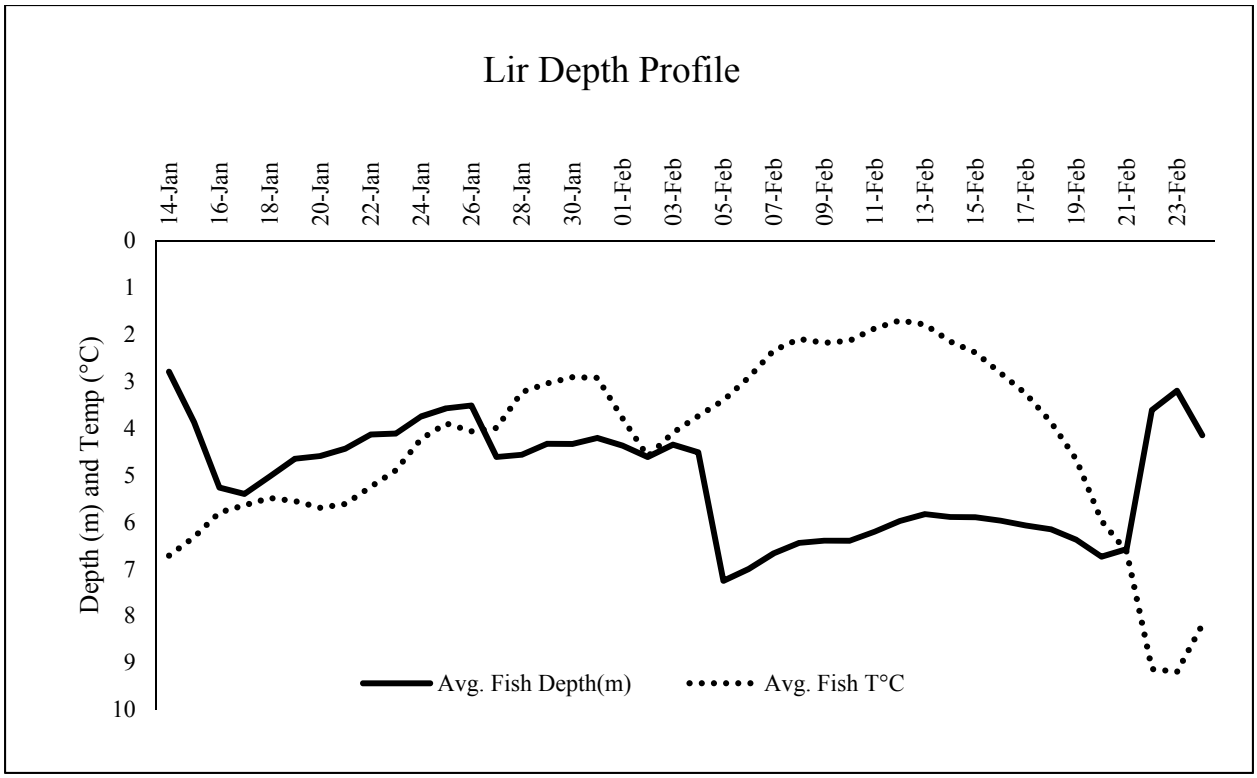

Figure 59. Average depth and temperature (°C) for Lir from January 14 to February 23

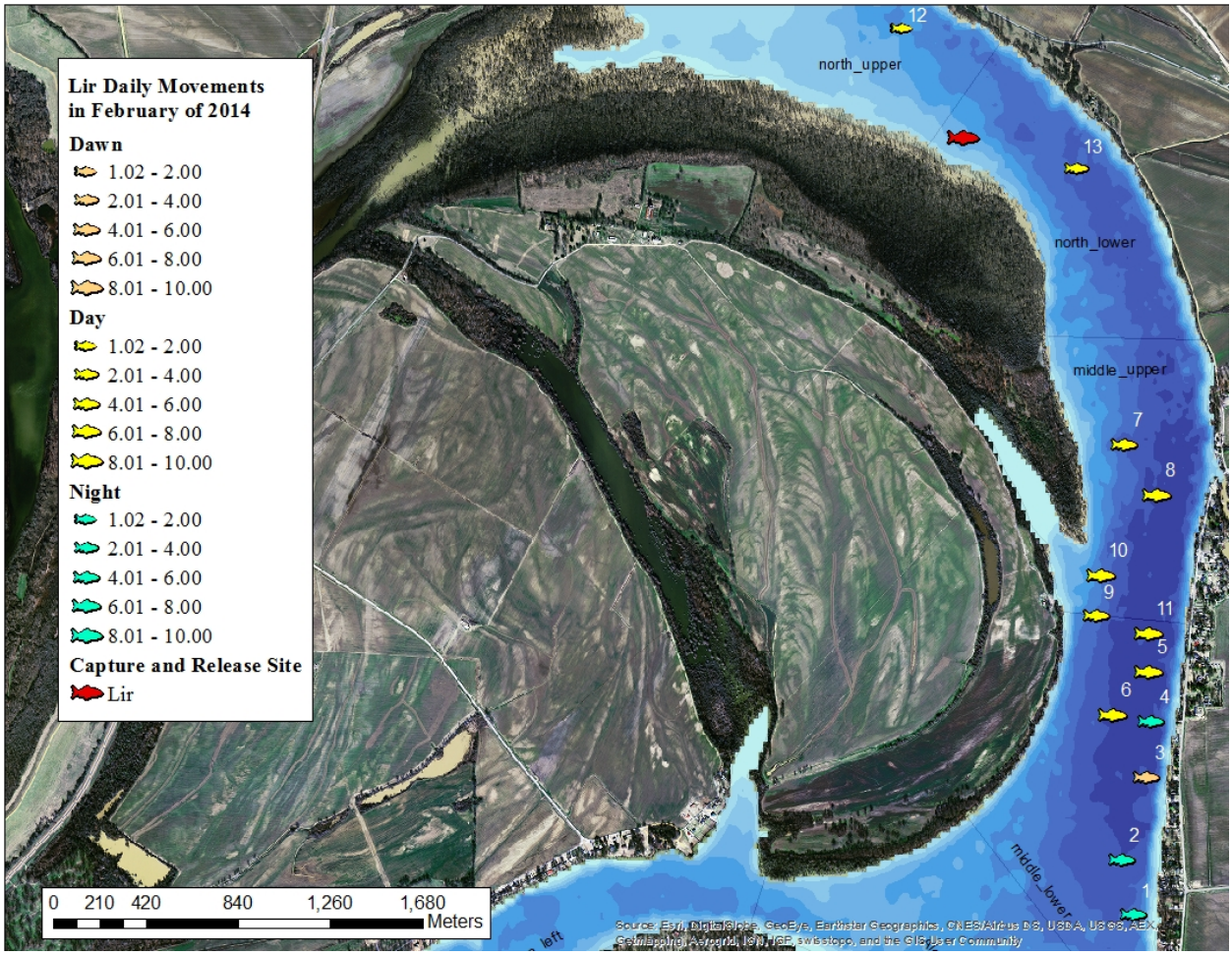

Figure 60. Daily movements of Lir during February of 2014

4.33 meters and an average temperature of 3.23°C. Several other paddlefish were located either in the area or less than a kilometer to the north. Galene entered the area a few hours after Lir, and Ceto was swimming a few kilometers to the north. On February 8 and 9 Lir had moved and occupied a small area of about 0.05 square kilometers in the north section of middle lower. The average depth and temperature was 6.43 meters and 2.10°C, respectively. Lir moved 1.24 kilometers to the north over the next week and was located again on February 15 in the very center of middle upper. Between February 15 and 17, Lir swam south to the border of middle upper and middle lower before advancing back to the north.

Neptune

Neptune weighed 17. 60 kilograms and had a calculated condition factor of 2.4. Eye-to-fork length was 901 mm and rostrum length was 362 mm (Table 21). Rostrum area was 385.17 cm^2 and the ratio of area to fish mass was 22.06 $cm^{2/}$/kg (Figure 61). The rostrum was slightly more rectangular than spatulate, but had a modest rostral shape index of 1.25. Neptune did not receive a depth and temperature archival tag. Neptune was released on January 1, 2014 at 34.41960 °N latitude and -90.51031°W longitude. Neptune was located 77% of the time in water that was greater than 7 meters. Of the 18 waypoints recorded for Neptune, 12 were located within middle lower (67%), 4 in middle upper (22.2%), and 2 in north lower (11.1%) (Figure 62). Neptune was first located on February 2 just before dusk at 0456 hrs. The paddlefish spent the entire day moving north arriving at the final waypoint which was taken at 2356 hr. at 34.44836°N latitude and -90.50067°W longitude. The straight line distance between the seven waypoints was 2.18 kilometers. The entire movement occurred in 19 hours and 2 minutes. This was the furthest point north Neptune was located during the study (Figure 63). Neptune was located a week later 3.18 kilometers to the south in the middle lower lake section. Over the next

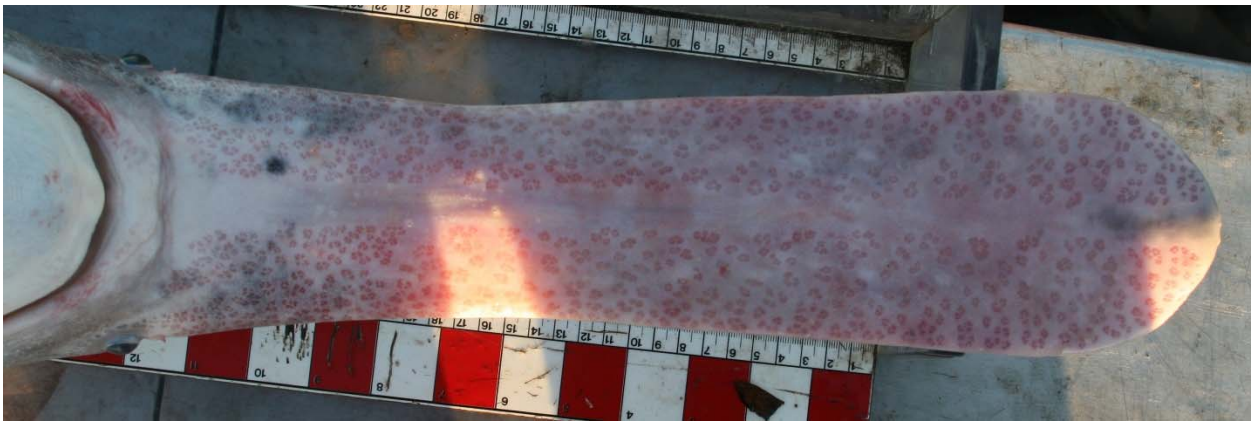

Figure 61. Photograph of Neptune's rostra

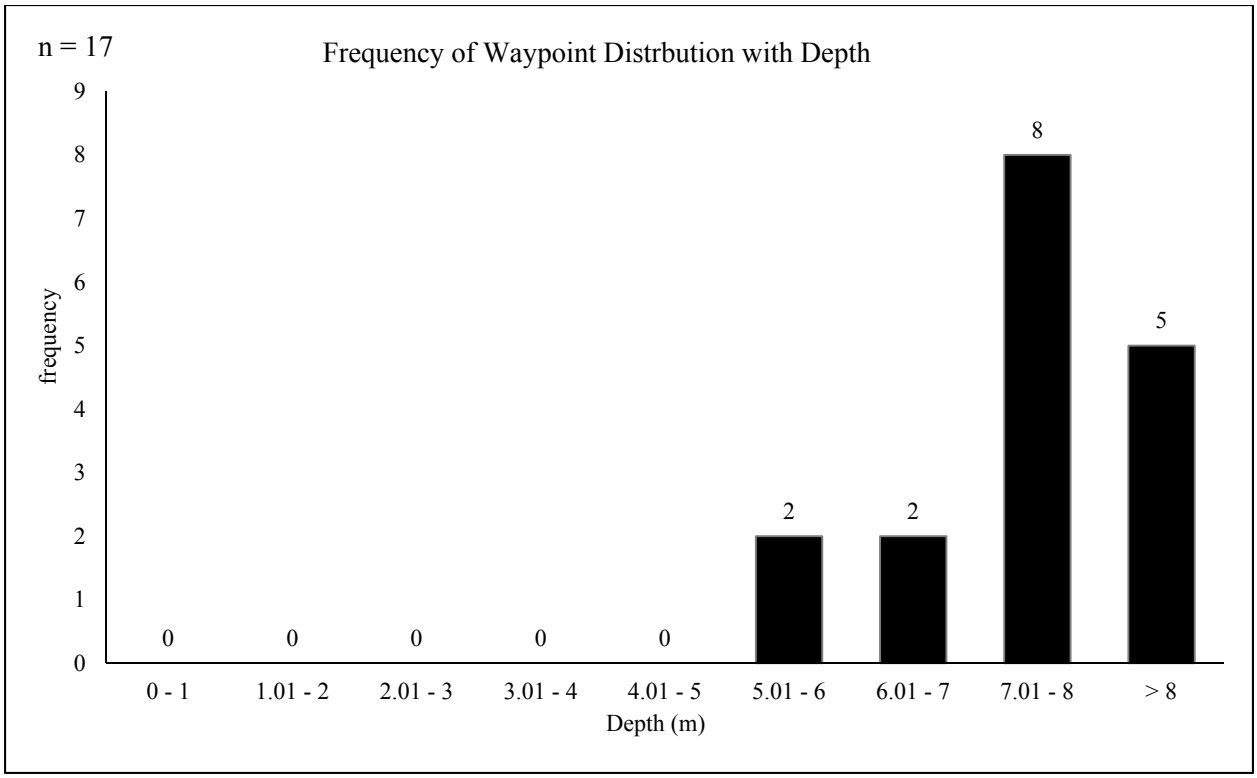

Figure 62. Frequency of waypoint distributions for Neptune grouped by lake depth

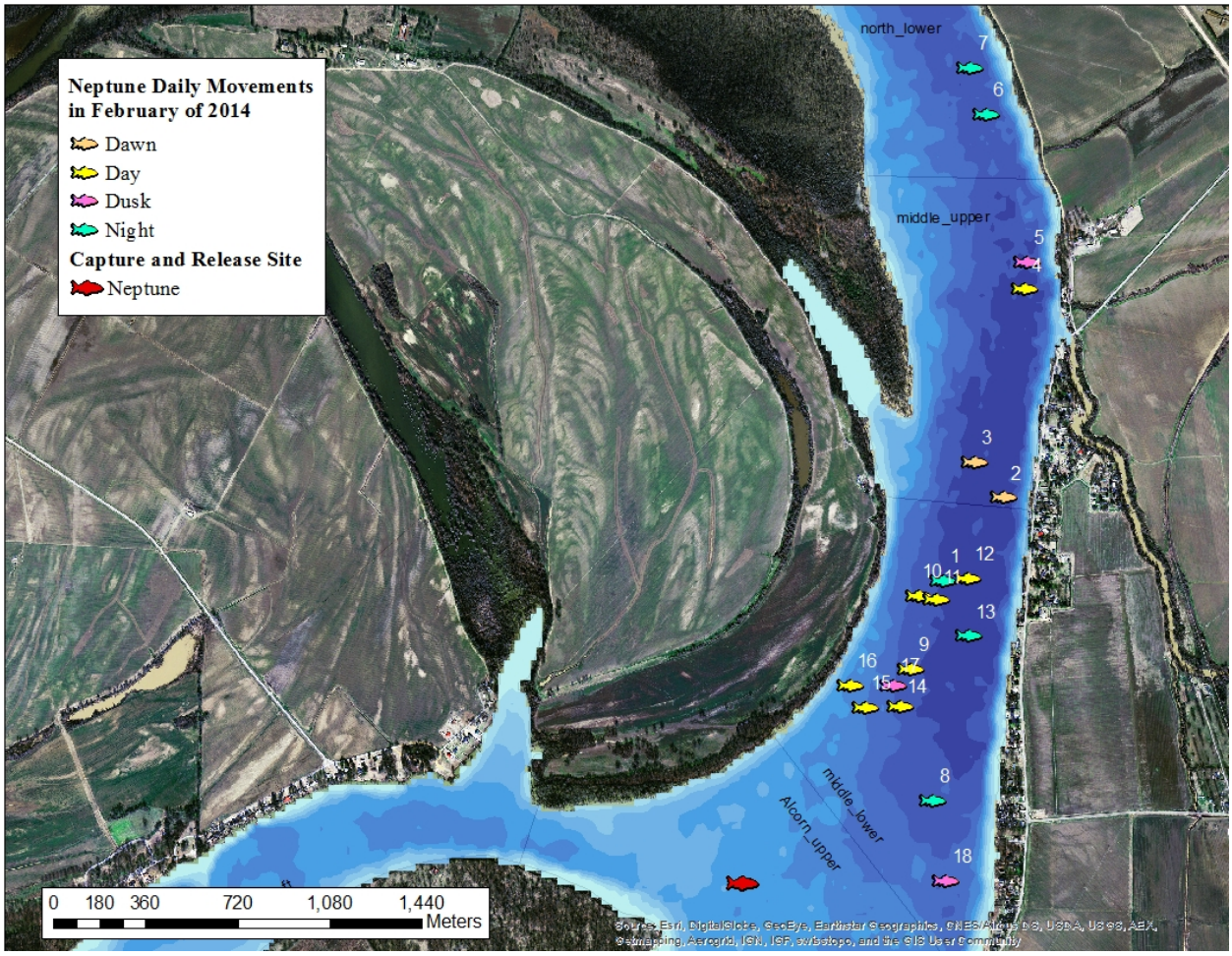

Figure 63. Daily movements of Neptune during February, 2014

two weeks (14 days) Neptune was located within an area spanning 0.25 km^2 with all points located within the middle lower lake section.

Nereus

Nereus weighed 35.01 kilograms and had a calculated condition factor of 2.4. Eye-to-fork length was 1136 mm and rostrum length was 418. The rostrum area was 460 cm^2 and the ratio of rostrum area to fish mass was 13.4 cm^2/kg. The rostral shape index was 1.34 (Table 21). This particular rostrum was a bit atypical. The longer the length the less tapering occurs from the tip to the base along the lateral borders (Figure 64).

Nereus was located a total of twenty-six times over a span of nine days beginning on January 31 and ending on February 23 (Figure 65). Nereus was located 1.48 kilometers to the northeast sixteen days following its release. Nereus began a slow movement north around midnight on January 31. Its northern displacement was just under a kilometer and it spent nearly 2 hours exploring the south portion of the middle upper lake section. Swimming was more exploratory than directional between waypoints 2, 3, and 4. At roughly six in the morning Nereus moved its efforts south/southeast to the eastern section of middle lower. The elapsed time was 2 hours and 44 minutes between waypoints 4 and 5 (Figure 65) covering a distance of 0.94 kilometers. Nereus returned north crossing the border between middle lower and middle upper seven days later. Over the next fourteen hours Nereus traveled a distance of 1.06 kilometers to the south returning once again into the middle lower section. On February 14 Nereus was located a short distance north in the upper reaches of middle lower at waypoint 9 (Figure 65). The zooplankton calories per cubic meter (a product of density and average calories per gram) was 19.6 cal/m^3 which was much lower than the February average of 73.8 cal/m^3. Over the night of February 14 to the midmorning of February 15 Nereus returned north to the deeper areas of

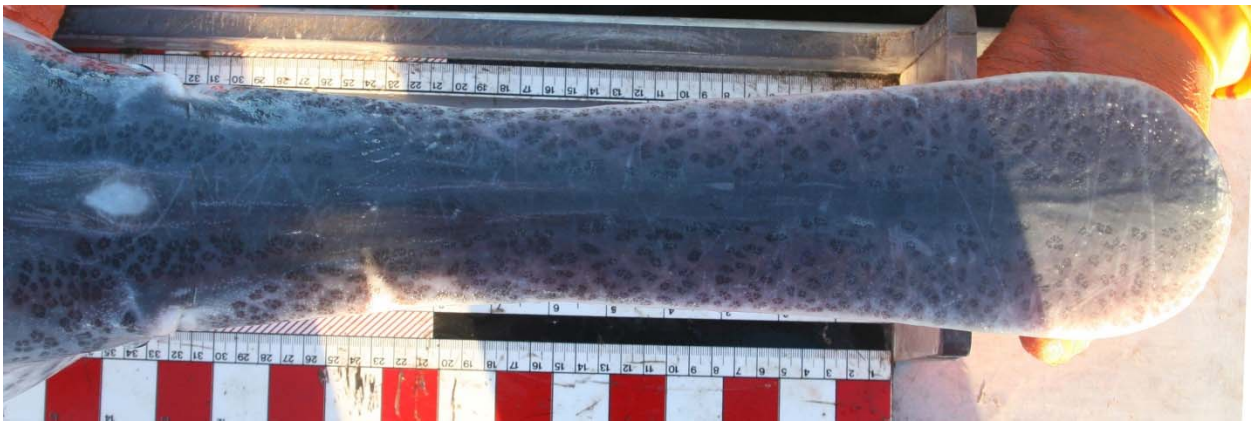

Figure 64. Photograph of Nereus's rostrum

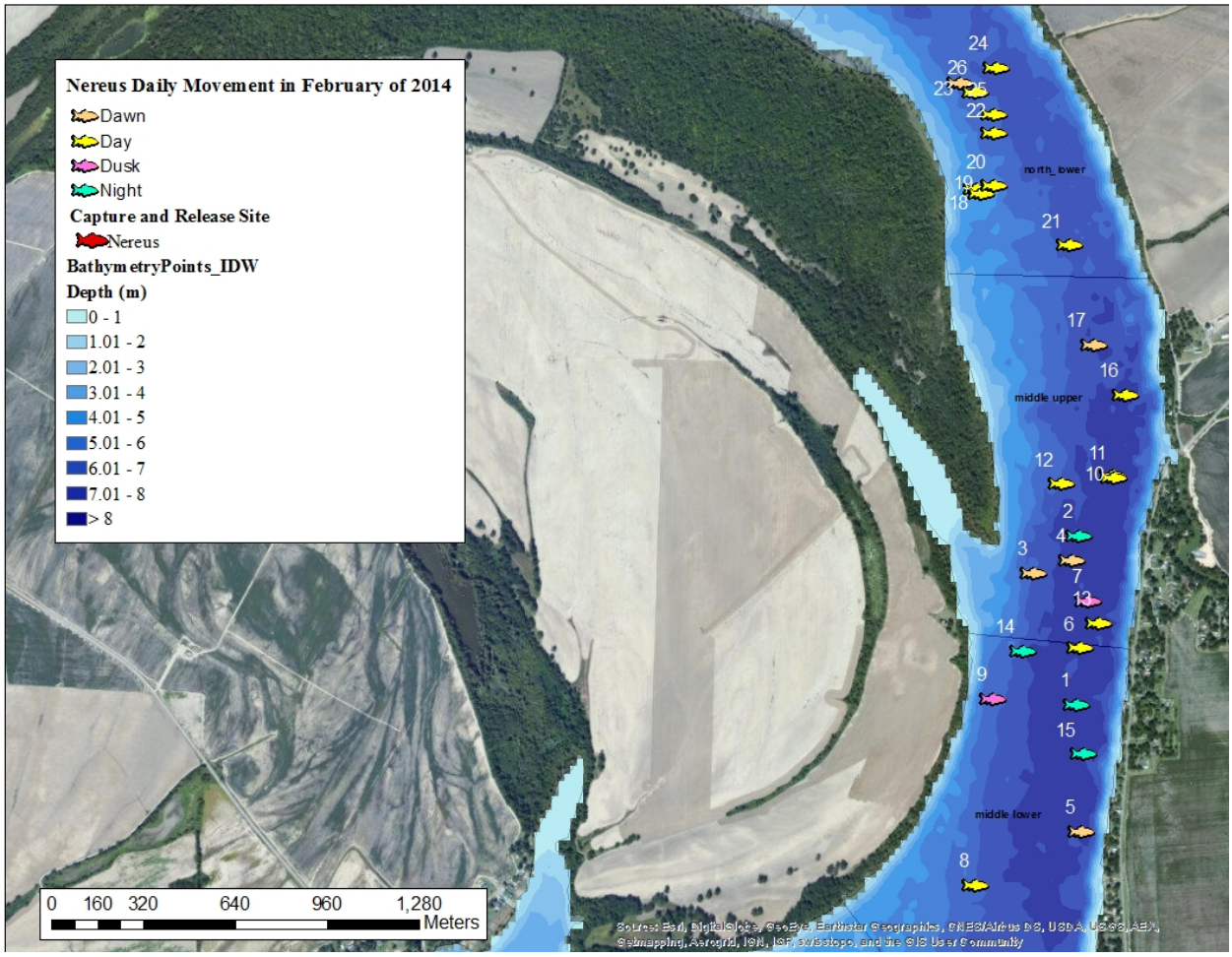

Figure 65. Daily movements of Nereus in February of 2014

middle upper. No information was available about its depth, but the average depth of other fish in the area was 7.22 meters. The caloric value of zooplankton sampled was low (7.22 cal/m^3). By 1645 hr. Nereus had moved to waypoint 13 (Figure 65) a half kilometer to the southeast. Between 1645 and 2317 hr. Nereus occupied a small area (0.045 km^2) on the border between middle upper and middle lower. The average caloric availability from zooplankton was 59.11 cal/m^3. The following morning (1024 hr.) Nereus was located (waypoint 16) 0.80 kilometers to the north. The surrounding calorie content was 78.58 cal/m^3. This value was around the average for February. On February 17 Nereus moved north and was located clustered in an area in the southwest section of north lower (waypoints 18, 19, and 20). It stayed in this small area for nearly three hours before being located 0.34 kilometers to the southeast (waypoint 21). Two days later on February 23 Nereus was located moving back and forth within an area in the middle of the north lower lake section. No zooplankton data was available for the surrounding area.

Poseidon

Poseidon weighed 25.63 kilograms and had a calculated condition factor of 1.91. Eye-to-fork length was 1103 and rostrum length was 382. The rostrum area was 309 cm^2 and the ratio of rostrum area to fish mass was 12.06 cm^2/kg. The rostrum was spatulate with a rostral shape index of 1.35 (Table 21). The release coordinates were not taken for Poseidon. The paddlefish was located a total of 8 times over 6 days (1//25, 2/1, 2/14, 2/15, 2/16, and 2/23). The first waypoint was taken on January 25 at 1553. The fish was swimming at a depth of 3.06 meters which was about 75% of the available depth. The average depth of Poseidon from January 15 to January 27 was 4.78 meters and the average temperature was 4.99°C (Figure 66). Poseidon was located again on February 2 (waypoint 2) at the southern border of middle upper swimming at a depth of 5.1 meters and a temperature of 3.25°C (Figure 67). Lake depth was 8.5 meters and the

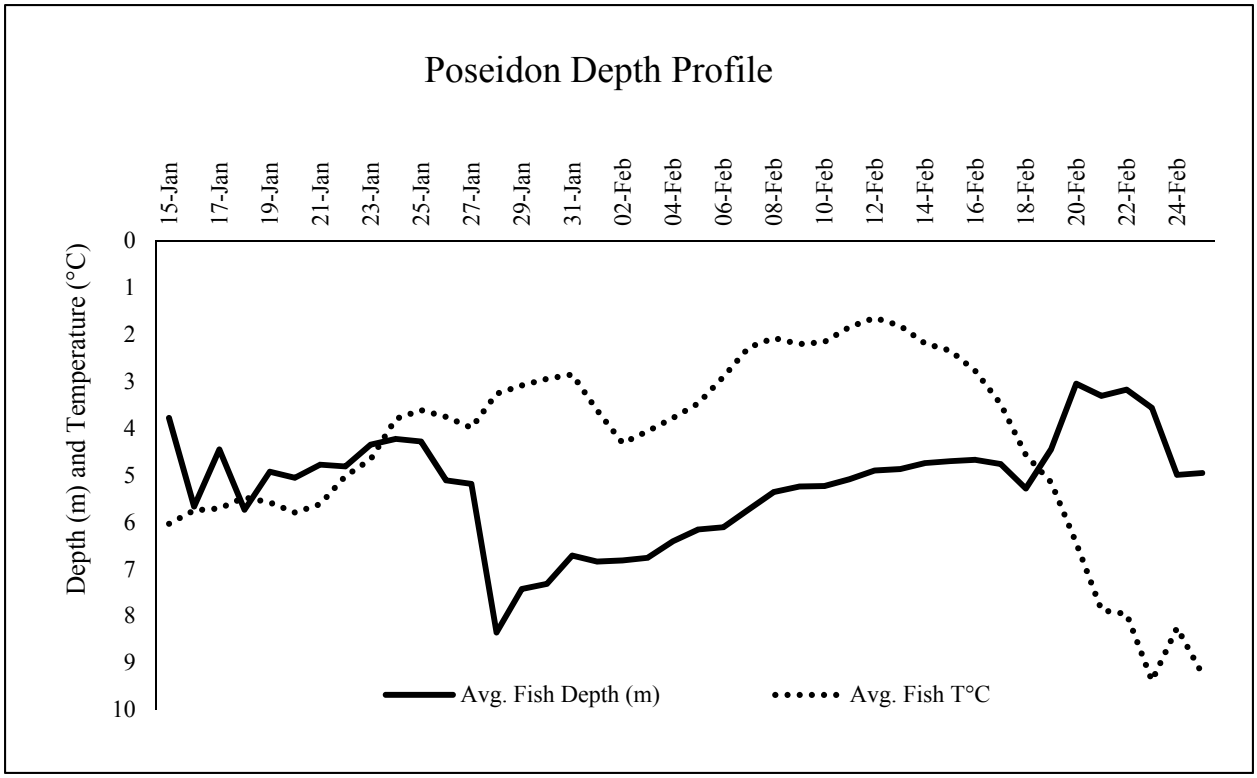

Figure 66. Average depth (m) and water temperature (°C) for Poseidon from January 15 to February 24

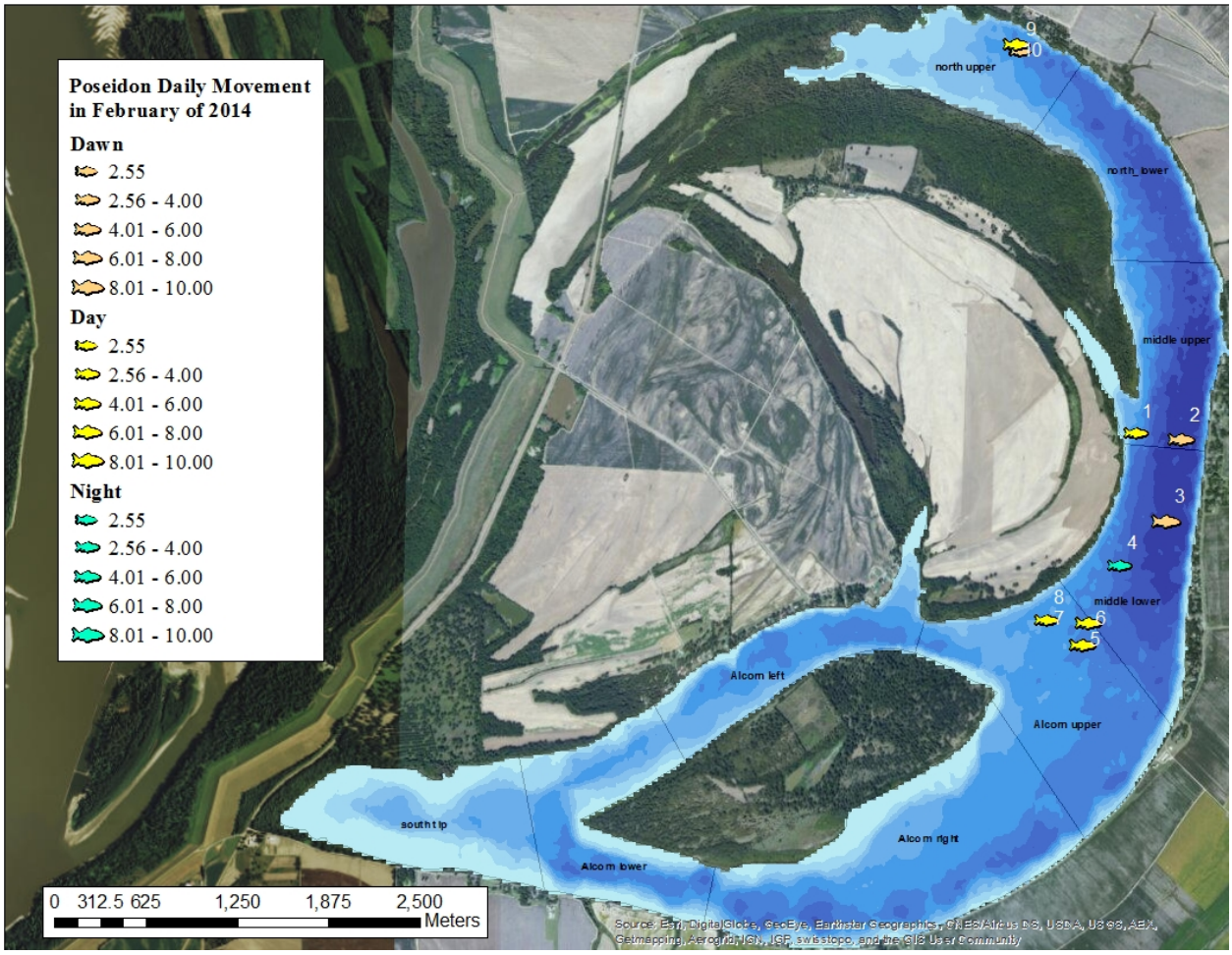

Figure 67. Daily movements of Poseidon in February, 2014

paddlefish was moving south. Poseidon was located again on February 14 in the middle lower section around midnight. The following day it was located four times during midday (waypoints 5, 6, 7, and 8). The caloric availability was seasonally high in the general area (107.18 cal/m^3) and this may be the reason for Poseidon staying in the area for twenty-four hours. The average depth of the fish over this period was 4.46 meters and the temperature was 2.27°C. Poseidon remained at an average of about 83% of lake depth. On February 23 Poseidon had traveled about 4.28 kilometers to the north up to the north upper lake section (waypoints 9 and 10). Three other paddlefish converged with Poseidon at a dense patch of zooplankton (Lir, Ahti, and Cymopoleia). The average density was around 490 organisms per cubic meter.

Speedo

Speedo was the first fish to be fitted with the ichthyometer (Chapter 5; Figure 111). It was 970 mm eye-to-fork length and had a rostrum length of 360 mm. This paddlefish was caught and released on May 3, 2014. It was located 35 times on 6 different days between May 4 and May 19. Eighty-three percent of all waypoint locations were recorded in middle upper, Alcorn upper, and Alcorn right lake sections (Figure 68). The fish was caught again on May 19 and the ichthyometer retrieved. The data unfortunately was corrupted. Speedo was first located after capture on May 4 at 0702 in Alcorn upper at a depth of 5 meters (Figure 69, waypoint 1). The calories per cubic meter of zooplankton in the water at this location was high at nearly 2,800 calories per cubic meter. At 1344 Speedo was located 1.77 kilometers to the southwest in the center of Alcorn right at a depth of 3.57 meters and a temperature of 19.33°C (Figure 69, waypoint 2). The fish returned north moving a straight line distance of 1.49 km. The location was on the eastern shore of Alcorn upper (Figure 69, waypoint 3). On May 9, Speedo was located 12 times between 1215 and 171l hours. The fish spent nearly 3 hours in an area ranging

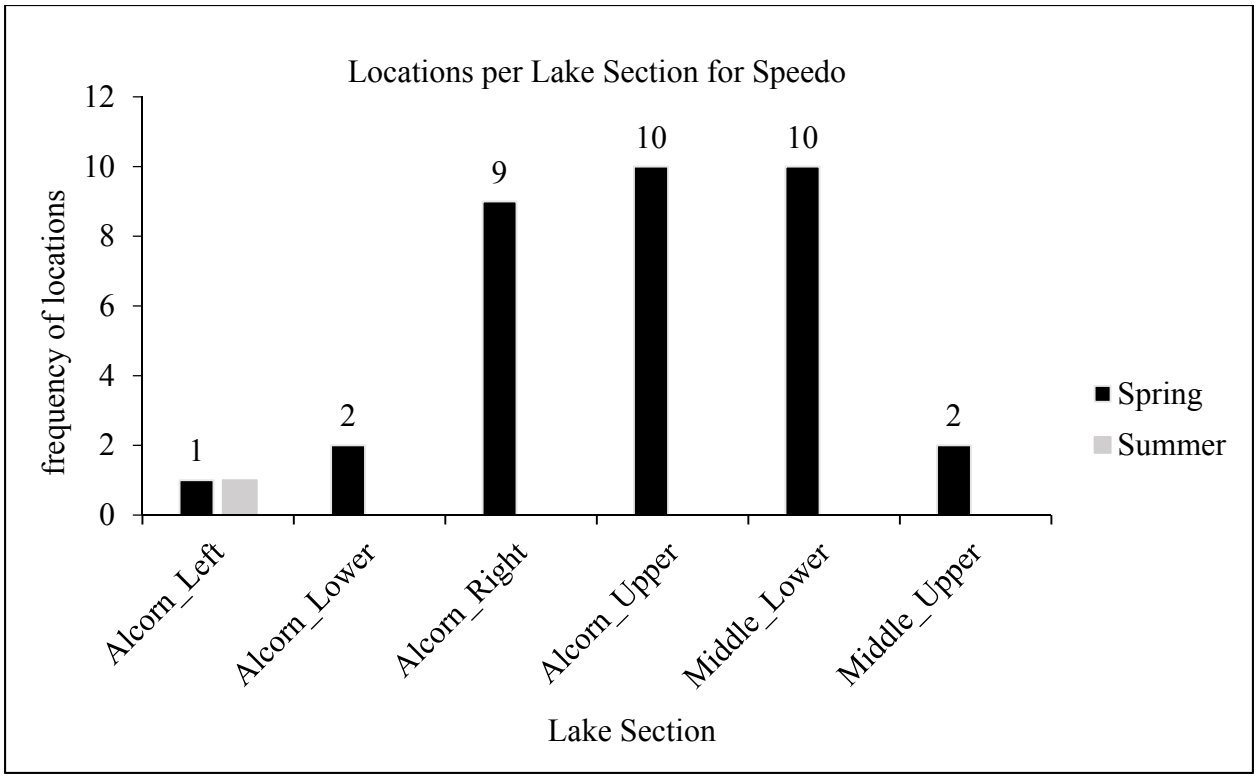

Figure 68. Frequencies of locations per lake section for Speedo during the spring of 2014

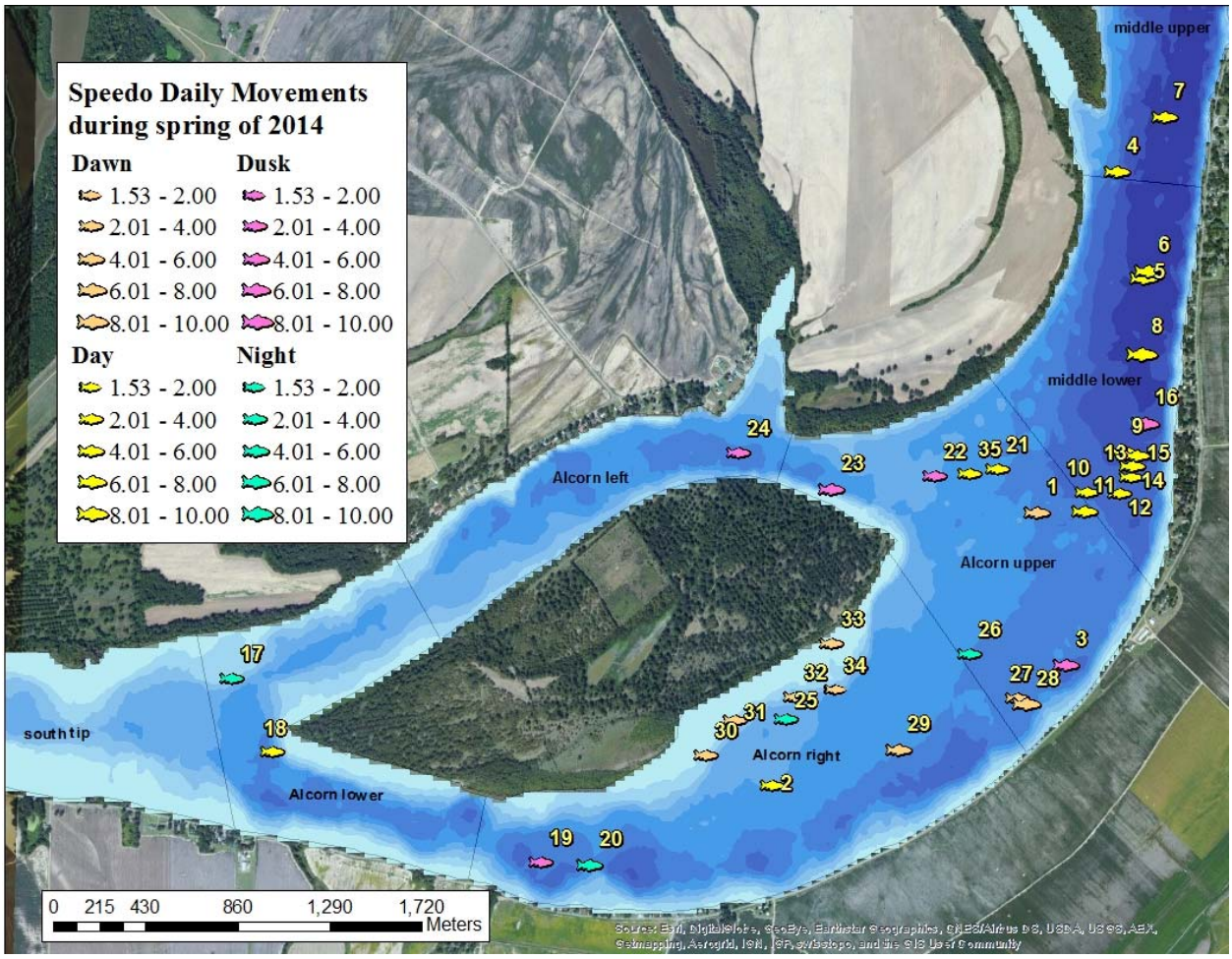

Figure 69. Daily movements of Speedo in May, 2014

from the border of middle upper to the middle section of middle lower (Figure 69, waypoints 4, 5, 6, 7, and 8). The area was nearly 0.11 square kilometers. It swam at an average depth of 5.53 meters and an average temperature of 21.84°C. The minimum depth was 1.53 meters and the maximum depth was 5.53 meters. At 1542 Speedo was located less than a kilometer to the south were it spent the next hour in the southeast corner of middle upper swimming at an average depth of 4.9 meters at 21.84°C (Figure 69, waypoints 9, 10, 11, 12, 13, 14, 15, and 16). The range of depth was from 2 to 5 meters. No zooplankton data was taken. On the 17th and 18th, Speedo circumnavigated around Alcorn Island. The fish was first located in a dense patch of zooplankton at the south end of the Island at 1623 (Figure 69, waypoint 18). The average density of zooplankton was 680 org/m^3. The caloric value was unknown. The average depth of Speedo was 3.4 meters at 20.9°C. The fish spent some time over the next hour near the surface at a depth of 0.51 meters. The maximum depth was 3.96 meters. Speedo was next located 1.35 km to the southeast as it began its way around into Alcorn right. Speedo spent the next hour and a half in this area over deeper waters. The average depth was about 4 meters or about 60% of the available depth. By the next afternoon Speedo had returned to the north of Alcorn Island and was located in the middle of Alcorn upper. Over the next 4 hours it swam west into Alcorn left. It swam at an average depth of 3.3 meters at 21.16°C, but vertical movements were highly variably ranging between one and six meters. The waypoint information is listed in Table 24.

Paddlefish Movements in March, 2014

Four fish were tagged in March of 2014: Hulk, Loki, Thor, and Wolverine. Weights and lengths were not taken prior to their release to reduce handling stress. The intention was to record data upon their capture. Wolverine was never located after its release and Hulk, Loki, and Thor were last located on 4/12, 4/21, and 5/19, respectively (Table 21).

Table 24. Waypoint information for Speedo in spring of 2014

Month - Day	Map ID	Time	Paddlefish ID	Lake Section	Lake Depth (m)
May-04	1	12:53:43	SPEEDO	Alcorn upper	8.49
May-04	2	14:10:31	SPEEDO	Alcorn right	8.51
May-04	3	15:26:21	SPEEDO	Alcorn upper	7.56
May-09	4	15:42:50	SPEEDO	Middle upper	6.57
May-09	5	16:06:35	SPEEDO	Middle lower	5.62
May-09	6	16:11:55	SPEEDO	Middle lower	5.36
May-09	7	16:32:46	SPEEDO	Middle upper	5.90
May-09	8	16:42:42	SPEEDO	Middle lower	6.47
May-09	9	16:45:23	SPEEDO	Middle lower	6.57
May-09	10	16:54:39	SPEEDO	Middle lower	6.85
May-09	11	17:11:50	SPEEDO	Alcorn upper	7.28
May-09	12	23:05:00	SPEEDO	Middle lower	3.20
May-09	13	16:23:00	SPEEDO	Middle lower	3.60
May-09	14	20:40:00	SPEEDO	Middle lower	4.40
May-09	15	22:11:00	SPEEDO	Middle lower	4.20
May-09	16	16:25:00	SPEEDO	Middle lower	4.30
May-16	17	18:02:00	SPEEDO	Alcorn lower	3.30
May-17	18	20:05:00	SPEEDO	Alcorn lower	4.20
May-17	19	20:44:00	SPEEDO	Alcorn right	4.20
May-17	20	03:48:00	SPEEDO	Alcorn right	3.30
May-18	21	04:52:00	SPEEDO	Alcorn upper	4.00
May-18	22	05:14:17	SPEEDO	Alcorn upper	4.90
May-18	23	05:21:57	SPEEDO	Alcorn upper	5.40
May-18	24	05:45:48	SPEEDO	Alcorn left	4.00
May-19	25	06:59:53	SPEEDO	Alcorn right	2.00
May-19	26	07:15:37	SPEEDO	Alcorn upper	1.40
May-19	27	07:32:05	SPEEDO	Alcorn upper	3.20
May-19	28	07:42:42	SPEEDO	Alcorn upper	2.40
May-19	29	07:54:01	SPEEDO	Alcorn right	3.20
May-19	30	11:21:00	SPEEDO	Alcorn right	3.80
May-19	31	12:53:43	SPEEDO	Alcorn right	8.49
May-19	32	14:10:31	SPEEDO	Alcorn right	8.51
May-19	33	15:26:21	SPEEDO	Alcorn right	7.56
May-19	34	15:42:50	SPEEDO	Alcorn right	6.57
May-19	35	16:06:35	SPEEDO	Alcorn upper	5.62

Hulk

Hulk was located 23 times on 6 separate days (3/30, 4/4, 4/5, 4/11, 4/12, and 4/13). On March 30, Hulk was located briefly in the lower half of north lower between 1400 and 1410 hours. On April 4, Hulk was located around 2135 in the eastern portion of middle upper just a short distance north of the entrance to the Yazoo Pass (Figure 70, waypoints 3 and 4). The caloric concentration of the water was 138 cal/m^3 with an average density of 4,068 org/m^3. Shortly after midnight on April 5 the paddlefish had moved to north lower and by 0210 was located just north of the border between north lower and middle upper (Figure 70, waypoints 5 and 6). The caloric concentration was much higher in this area at 287 cal/m^3 and and average density of 4,876 org/m^3. By 1110 Hulk was located 2.5 kilometers to the south. For the next six hours Hulk spent time moving north and south back and forth between middle lower and Alcorn upper (Figure 70, waypoints 7, 8, 9, 10, 11, and 12). The caloric concentration in Alcorn upper (101 cal/m^3) at 1529 was lower than the caloric concentrations in middle upper (261 cal/m^3) at 1719. On April 11, Hulk was located in the west section of middle lower. Over the next 24 hours it moved into Alcorn right and looped back up the eastern shore of Alcorn Island. The total distance between waypoints was nearly 5 kilometers (Figure 70). On April 13, Hulk initially covered a long distance over 2 hours moving from Alcorn upper to middle upper between 1104 and 1313 hours. The caloric concentration at the middle upper location was 99 cal/m^3. Over the course of 5 hours Hulk moved from to the northern border of middle upper spending alittle over an hour in the area. The caloric concentration dropped from 135 to 65 cal/m^3 during this time. Hulk left the area and was located 1.2 kilometers to the south just below the southern border of middle upper. The caloric concentration was even lower in this area at 22 cal/m^3. The last time

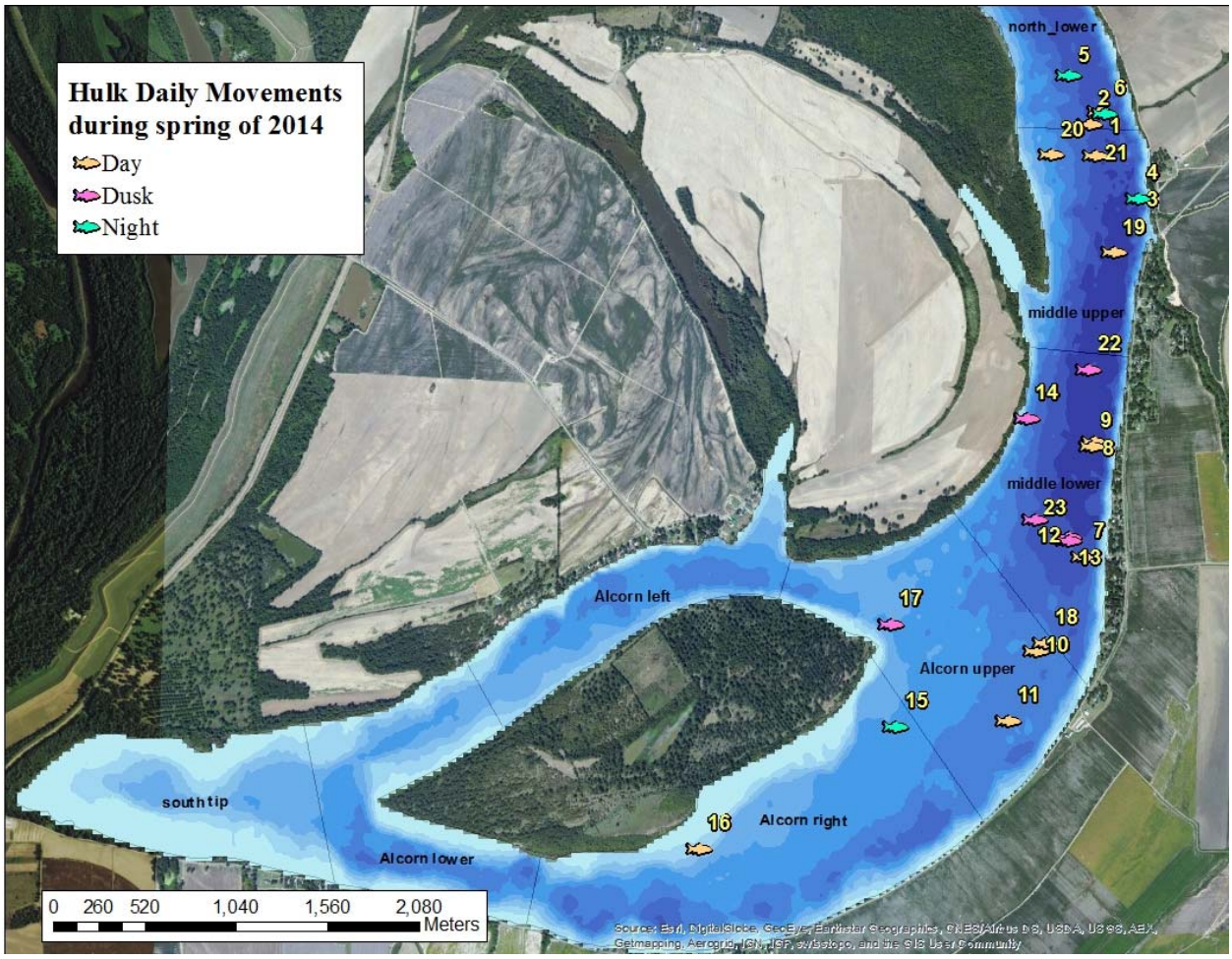

Figure 70. Daily movements of Hulk in spring, 2014

Hulk was located was on April 12 nearly a kilometer to the southwest at 1818 in middle upper (Table 21). The waypoint information is listed in Table 25.

Loki

Loki was located 10 times on 5 separate days in March and April. Loki was located twice in Alcorn upper on March 23 at 1400 and 1421 hours. This distance between locations was only 0.29 kilometers. On March 29 Loki was located in the western portion of north lower. The fish moved over the next 5.5 hours to Alcorn upper close to the location it had recorded just six days earlier (Figure 71, waypoints 3 and 4). Over the next nine hours Loki returned north moving just across the border into north lower. The caloric concentration and zooplankton density were the highest recorded during the spring at 492 cal/m^3 and 12,199 organisms per cubic meter, respectively. It should be noted that Thor was also in the area at 1121 and Hulk was located close by just three hours later.

On April 5, Loki was again located at the border of north lower and middle upper. The caloric concentration and zooplankton densities were again moderately high at 329 cal/m^3 and 7,966 org/m^3, respectively. Hulk was located 0.24 kilometers to the northeast just one hour prior to this location. The caloric concentrations (287 cal/m^3) and zooplankton densities (4,876 org/m^3) in that area were also moderately high for the spring. At 1635 Loki had moved 0.70 kilometers to the northwest and was located in the western portion of north lower were it had been located previously on March 29 (Figure 71, waypoint 9). The caloric concentration was 142 calories per cubic meter. The last location during this study was on April 12, 2014 in north upper at 1605. This was the furthest north Loki had been found. The waypoint information is listed in Table 26.

Table 25. Waypoint information for Hulk in spring of 2014

Month - Day	Map ID	Time	Paddlefish ID	Lake Section	Lake Depth (m)
30-Mar	1	14:00:46	HULK	North lower	--
	2	14:10:04	HULK	North lower	--
04-Apr	3	21:34:30	HULK	Middle upper	7.90
	4	21:35:07	HULK	Middle upper	7.90
05-Apr	5	00:30:57	HULK	North lower	6.76
	6	02:10:24	HULK	North lower	7.80
	7	11:10:46	HULK	Middle lower	7.30
	8	12:48:26	HULK	Middle lower	8.28
	9	12:50:05	HULK	Middle lower	--
	10	14:13:33	HULK	Alcorn upper	5.34
	11	15:29:27	HULK	Alcorn upper	5.00
	12	17:07:36	HULK	Middle lower	7.40
	13	17:08:03	HULK	Middle lower	7.47
11-Apr	14	17:31:12	HULK	Middle lower	4.53
	15	23:23:26	HULK	Alcorn right	4.08
12-Apr	16	14:08:17	HULK	Alcorn right	3.11
	17	17:00:45	HULK	Alcorn upper	3.94
13-Apr	18	11:04:00	HULK	Alcorn upper	5.53
	19	13:13:53	HULK	Middle upper	8.23
	20	14:19:30	HULK	Middle upper	4.74
	21	15:31:06	HULK	Middle upper	7.54
	22	17:13:24	HULK	Middle lower	9.13
	23	18:18:33	HULK	Middle lower	6.57
				Grand Total	6.43

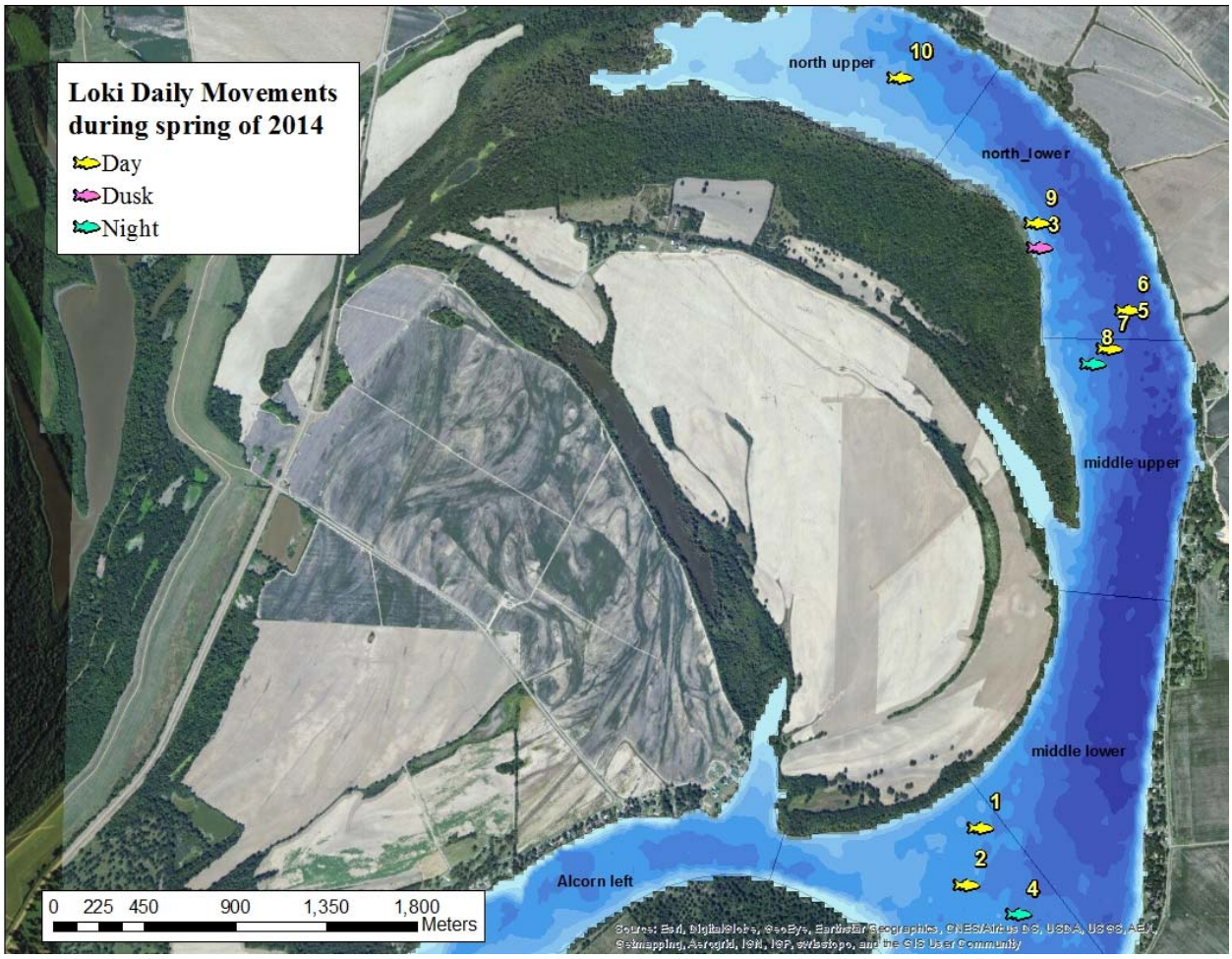

Figure 71. Daily movements of Loki in spring, 2014

Table 26. Waypoint information for Loki in spring of 2014

Month - Day	Map ID	Time	Paddlefish ID	Lake Section	Lake Depth (m)
Mar - 23	1	14:00:56	LOKI	Alcorn upper	--
	2	14:21:36	LOKI	Alcorn upper	--
Mar - 29	3	19:13:44	LOKI	North lower	2.30
Mar - 30	4	00:47:21	LOKI	Alcorn upper	5.19
	5	10:10:02	LOKI	North lower	7.40
	6	10:10:12	LOKI	North lower	7.40
	7	11:15:27	LOKI	Middle upper	6.30
Apr - 05	8	03:12:20	LOKI	Middle upper	5.46
	9	16:35:36	LOKI	North lower	4.08
Apr - 12	10	16:05:11	LOKI	North upper	3.70
				Grand Total	5.23

Thor

Thor was located several times on March 22 and 29 (Figure 72). On March 30 it was located nine times from 1311 and 1935 hours. Eight of the nine locations were recorded in the upper northeast corner of north upper. Thor was located a solitary time just below the border of north upper and north lower at 1035. One hundred and eight calories per cubic meter was recorded from a single zooplankton tow taken at 1808 (Figure 72, waypoint 11). The waypoint information for March is listed in Table 27.

Thor was located only four times on two separate days on April 4 and 11 (Figure 73, waypoints 13, 14, 15, and 16). The paddlefish was located in middle upper heading south shortly after dusk on the 4th. On April 11 it made a lengthy movement from north lower to middle lower in roughly one hour and fifteen minutes swimming at a velocity of 133 cm/s to an area with a caloric concentration of 124 calories per cubic meter. The following day on the 12th, the fish was located three times along the eastern edge of middle lower (Figure 73, waypoint 25). The stay was short as the fish turned north into more prosperous waters of middle upper (205 cal/m^3). The last locality of April 13 was taken at the southeast portion of middle lower where the fish had been located just 3 hours prior.

Thor was located 7 times on the evening and morning of April 26 and 27. The paddlefish was first located in middle upper (waypoint 28) around 2211. The caloric concentration was lower at about 110 calories per cubic meter and the density was 2,476 org/m^3. The fish was moving south. At 2316 it had reached the border between middle upper and middle lower (waypoint 29). The zooplankton concentration was much higher (300 cal/m^3) in this area than the locality to the north just two hours prior. Thor continued south and reached the middle of middle lower around 0014 (waypoint 30). The caloric concentration in the area was a bit lower than the

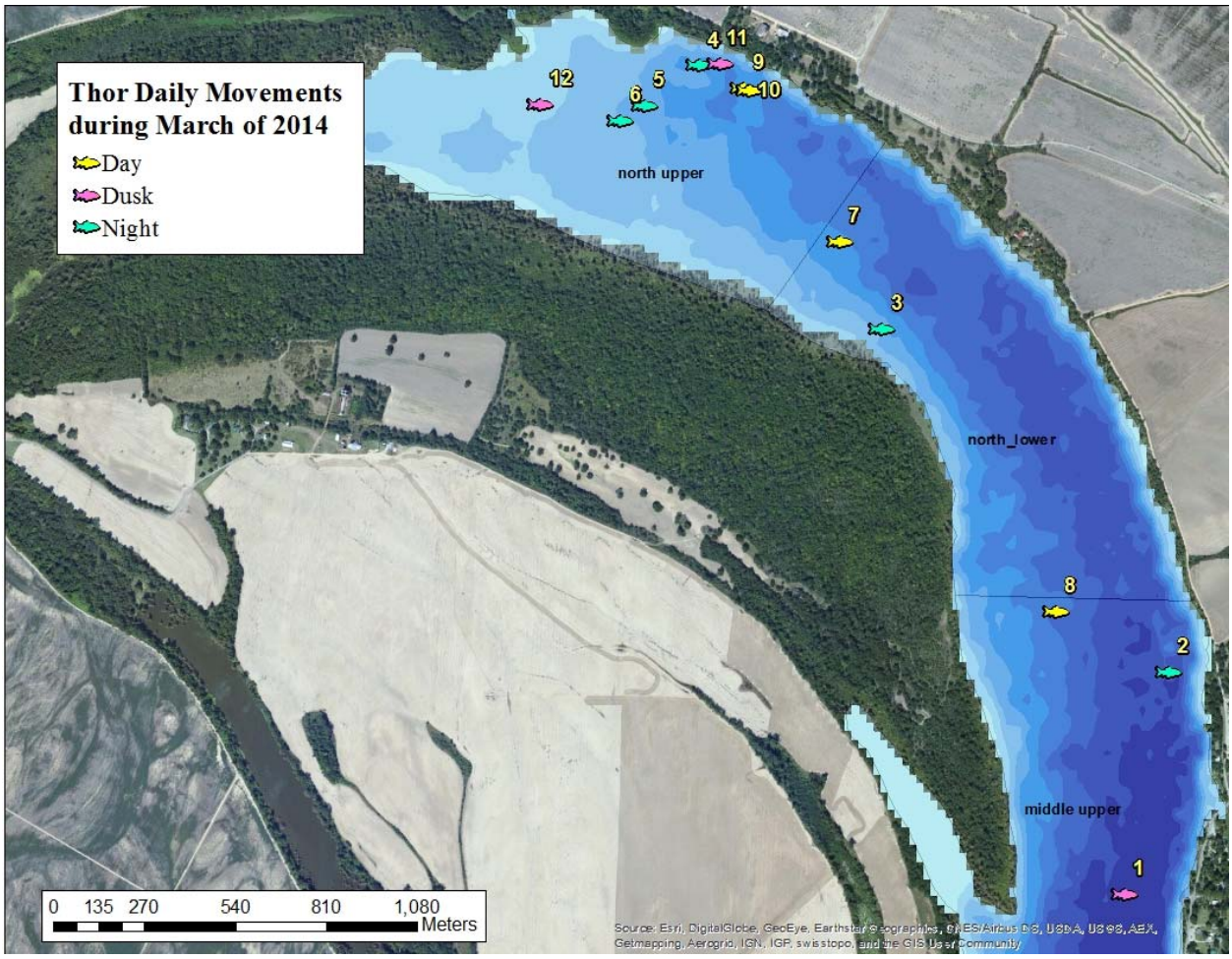

Figure 72. Daily movements of Thor in March, 2014

Table 27. Waypoint information for Thor in March of 2014

Month - Day	Map ID	Time	Paddlefish ID	Lake Section	Lake Depth (m)
Mar- 22	1	18:52:03	THOR	Middle upper	--
Mar- 29	2	21:20:58	THOR	Middle upper	8.06
	3	23:55:40	THOR	North lower	3.37
Mar- 30	4	01:11:38	THOR	North upper	3.63
	5	02:12:13	THOR	North upper	2.96
	6	02:25:23	THOR	North upper	2.61
	7	10:35:14	THOR	North lower	4.70
	8	11:21:00	THOR	Middle upper	5.98
	9	12:41:00	THOR	North upper	4.13
	10	12:41:26	THOR	North upper	4.20
	11	18:05:50	THOR	North upper	3.70
	12	19:35:27	THOR	North upper	1.40

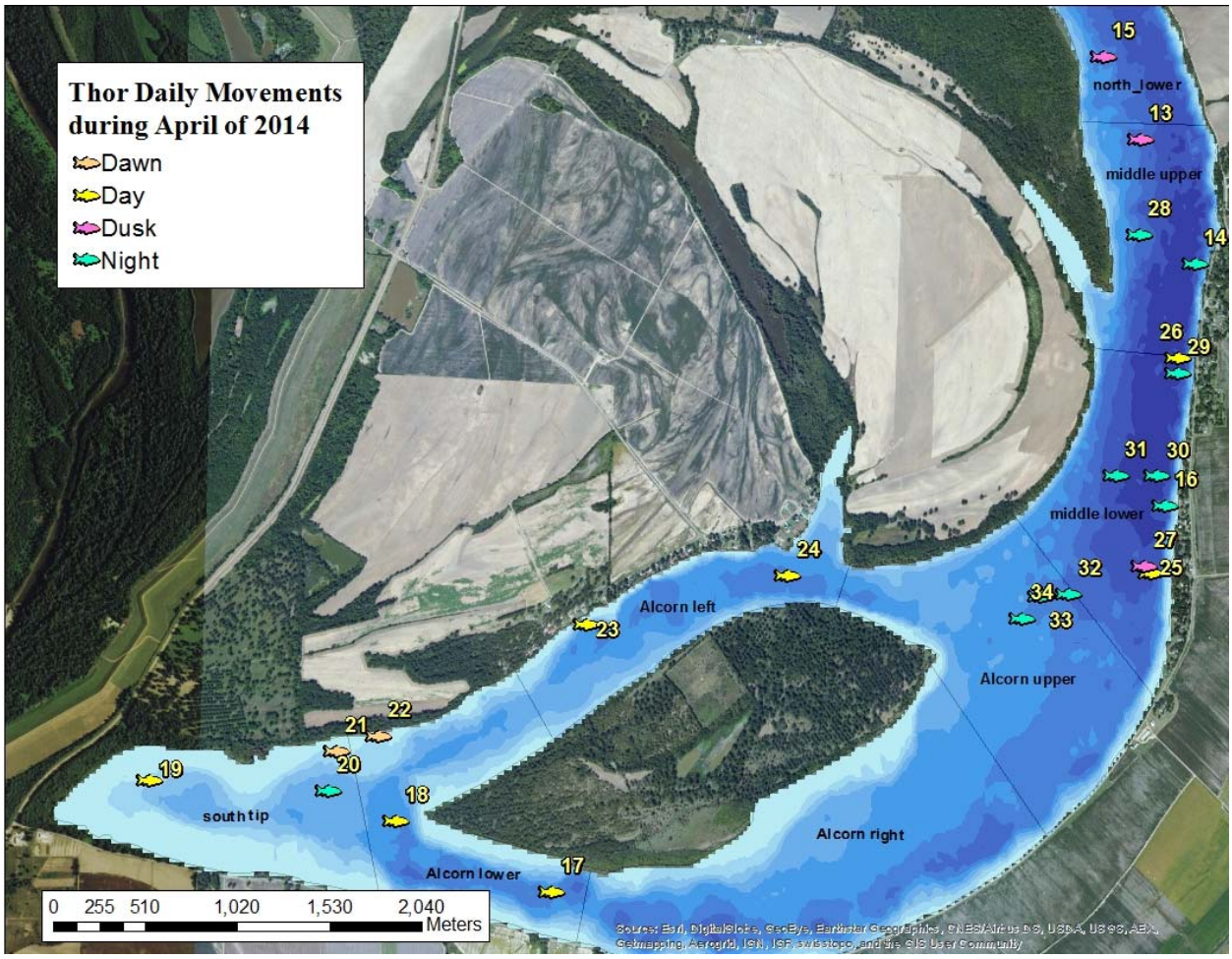

Figure 73. Daily movements of Thor in April, 2014

previous location. The concentration was 216 cal/m^3 and the density was 8,733 organisms per cubic meter. Thor traveled a short distance west to the center of middle upper before heading south at 0047. From 0200 to 0443 Thor spent time on the border between Alcorn upper and middle lower. The caloric concentration was moderate at 281cal/m^3 with a density of 5,326 org/m^3. The waypoint information for April is listed in Table 28.

On May 4, Thor was located 6 times between 0601 to 1719 hours (Figure 74, waypoints 35, 36, 37, 38, 39, and 40). At dawn Thor was located just south of the border between middle upper and middle lower. The caloric concentration was 117 cal/m^3. Over the next 6.5 hours Thor was located 4 times in the upper to middle regions of middle lower. The caloric concentration averaged 84 calories per cubic meter. The total area enveloped by the four waypoint locations was 0.38 km^2. At 1442 Thor moved 1.36 kilometers into the upper half of middle upper (waypoints 39 and 40) where the caloric concentration was much lower. It averaged 45.5 cal/m^3 over 2.5 hours from 1441 to 1719 hours. On May 8, Thor was located in the upper reaches of the lake. At 1933 it was located in the north part of north upper in water less than 3 meters deep. No zooplankton data was recorded, but the paddlefish remained in this small area (0.03 km^2) for the better part of an hour before moving east (Figure 74, waypoints 41, 42, and 43).

Movements on May 16, 17, 18, and 19 were long covering nearly half the lake. On May 16 the fish moved 1.9 kilometers from middle upper down to the border of Alcorn upper and middle lower. The fish was subsequently located one time on each of the next three days. The distances were very long stretching nearly the entire upper half of the lake and back. From May 16 to May 17 the fish had moved 1.86 kilometers to the southwest moving from Alcorn upper into Alcorn right. Within nine hours the fish had moved 5.6 kilometers up to the upper section of north lower on April 18. Thirteen hours later the fish was once again down 3.6 kilometers to the

Table 28. Waypoint information for Thor in April of 2014

Month - Day	Map ID	Time	Paddlefish ID	Lake Section	Lake Depth (m)
Apr- 04	13	19:42:10	THOR	Middle upper	6.38
	14	23:25:10	THOR	Middle upper	8.47
Apr- 11	15	19:45:41	THOR	North lower	5.12
	16	21:59:20	THOR	Middle lower	7.69
Apr- 12	17	10:09:29	THOR	Alcorn lower	4.34
	18	11:31:51	THOR	Alcorn lower	3.89
	19	14:35:57	THOR	South tip	2.23
Apr- 13	20	04:37:41	THOR	South tip	5.27
	21	06:06:11	THOR	South tip	3.04
	22	08:59:59	THOR	Alcorn lower	3.34
	23	10:12:03	THOR	Alcorn left	4.29
	24	11:31:01	THOR	Alcorn left	4.58
	25	15:07:35	THOR	Middle lower	7.28
	26	16:46:20	THOR	Middle lower	8.63
	27	18:04:11	THOR	Middle lower	7.40
Apr- 26	28	22:11:04	THOR	Middle upper	5.76
	29	23:16:15	THOR	Middle lower	8.15
Apr- 27	30	00:14:15	THOR	Middle lower	7.89
	31	00:47:57	THOR	Middle lower	6.97
	32	02:00:29	THOR	Alcorn upper	5.69
	33	03:10:33	THOR	Alcorn upper	4.98
	34	04:43:43	THOR	Alcorn upper	4.60

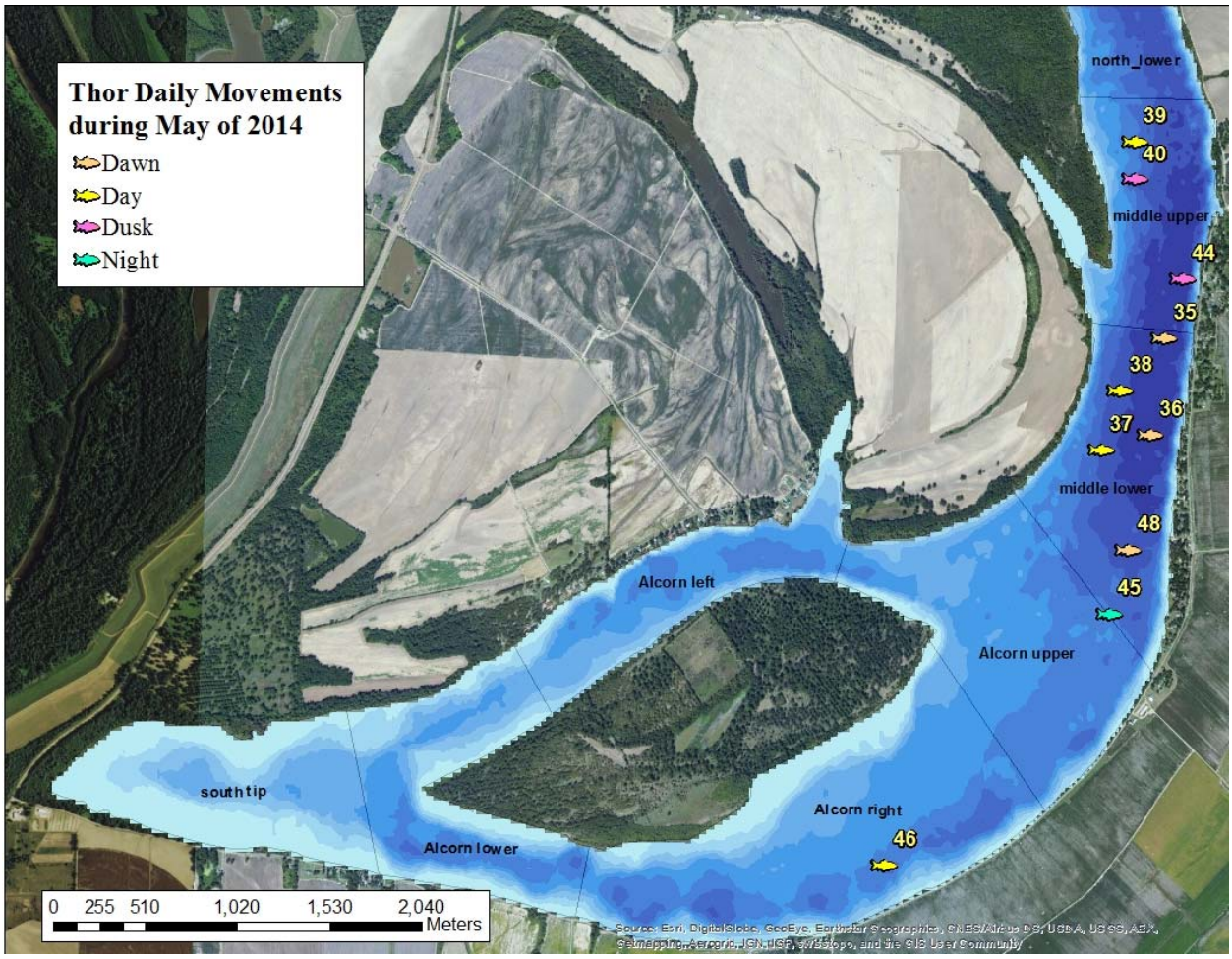

Figure 74. Daily movements of Thor in May, 2014

south in middle lower (Figure 74 waypoints 46, 47, 48, and 49). The paddlefish was last located on May 19, 2014 (Table 21). The waypoint information for May is listed in Table 29. Waypoint information for Thor in May of 2014.

Alittlehigh

Alittlehigh was located 7 times between May 5 and July 21. The fish was tagged on May 3, 2014. The first waypoint was recorded on May 5 at 2159 in Alcorn upper just to the northeast of Alcorn Island. The fish was in the area for at least an hour and a half. All other locations were recorded on separate days without two locations occurring on the same day. Alittlehigh was last located on July 21, 2014 (Table 21). Locations and times are listed in Table 30 and are shown in Figure 75.

Amedhigh

Amedhigh was located 6 times between May 8 and June 14. The fish was tagged on May 3, 2014. A couple of waypoints were recorded on May 8 in Alcorn upper at 2208 and 2316 hours. Amedhigh was located once on May 17 in middle lower and once again on May 19 in middle upper (Figure 76). The last day that Amedhigh was located in the lake was on June 14. At 0157, Amedhigh was located in middle lower. The second waypoint was located 0.97 kilometers to the north in middle upper at 1152. The last date the fish was located was June 14, 2014. Locations and times are listed in Table 30 and are shown in Figure 76.

Speedo 2

Speedo2 was tracked during September, 2014. It was the third paddlefish to be fitted with an “ichthyometer” and was tracked from September 10 to September 21 before the unit detached from the fish. It was tagged and released on September 1. As of the time of this writing the

Table 29. Waypoint information for Thor in May of 2014

Month - Day	Map ID	Time	Paddlefish ID	Lake Section	Lake Depth (m)
May- 04	35	06:01:00	THOR	Middle lower	8.94
	36	07:30:22	THOR	Middle lower	8.56
	37	09:08:44	THOR	Middle lower	6.47
	38	12:22:05	THOR	Middle lower	7.16
	39	14:41:54	THOR	Middle upper	5.59
	40	17:19:14	THOR	Middle upper	5.36
May- 08	41	19:33:36	THOR	North upper	2.82
	42	20:42:44	THOR	North upper	2.79
	43	22:51:03	THOR	North upper	3.77
May- 16	44	20:08:00	THOR	Middle upper	8.50
	45	22:20:00	THOR	Middle lower	5.40
May- 17	46	10:19:00	THOR	Alcorn right	4.70
May- 18	47	18:41:00	THOR	North lower	5.00
May- 19	48	08:05:43	THOR	Middle lower	7.10
				Grand Total	5.38

Table 30. Waypoint information for Alittlehigh and Amedhigh in spring of 2014

Month - Day	Map ID	Time	Paddlefish ID	Lake Section	Lake Depth (m)
May-08	1	21:59:23	ALITTLEHIGH	Alcorn upper	3.4
	2	23:23:40	ALITTLEHIGH	Alcorn upper	3.7
May-17	3	14:38:00	ALITTLEHIGH	North lower	5.5
May-18	4	18:23:00	ALITTLEHIGH	Middle upper	8.1
June-14	5	09:43:00	ALITTLEHIGH	Alcorn right	4.1
July-20	6	20:53:34	ALITTLEHIGH	North lower	5.2
July-21	7	07:00:09	ALITTLEHIGH	North lower	6.9
May-08	1	22:08:33	AMEDHIGH	Alcorn upper	3.8
	2	23:16:56	AMEDHIGH	Alcorn upper	3.6
May-17	3	15:20:00	AMEDHIGH	Middle lower	6.2
May-19	4	08:10:23	AMEDHIGH	Middle lower	8.1
June-14	5	01:57:00	AMEDHIGH	Middle lower	8.1
	6	11:52:00	AMEDHIGH	Middle upper	8.6

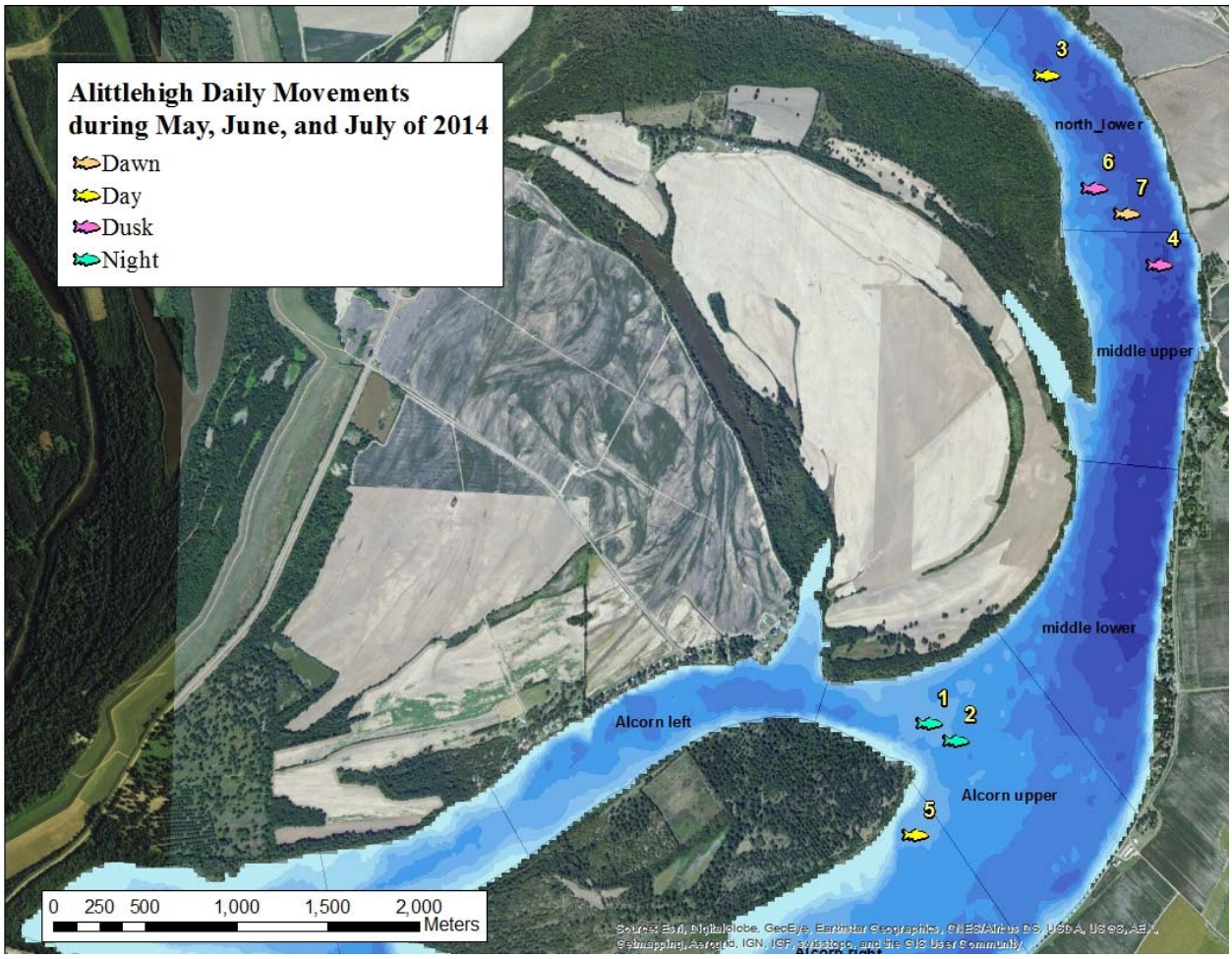

Figure 75. Daily movements of Alittlehigh in May, June, and July, 2014

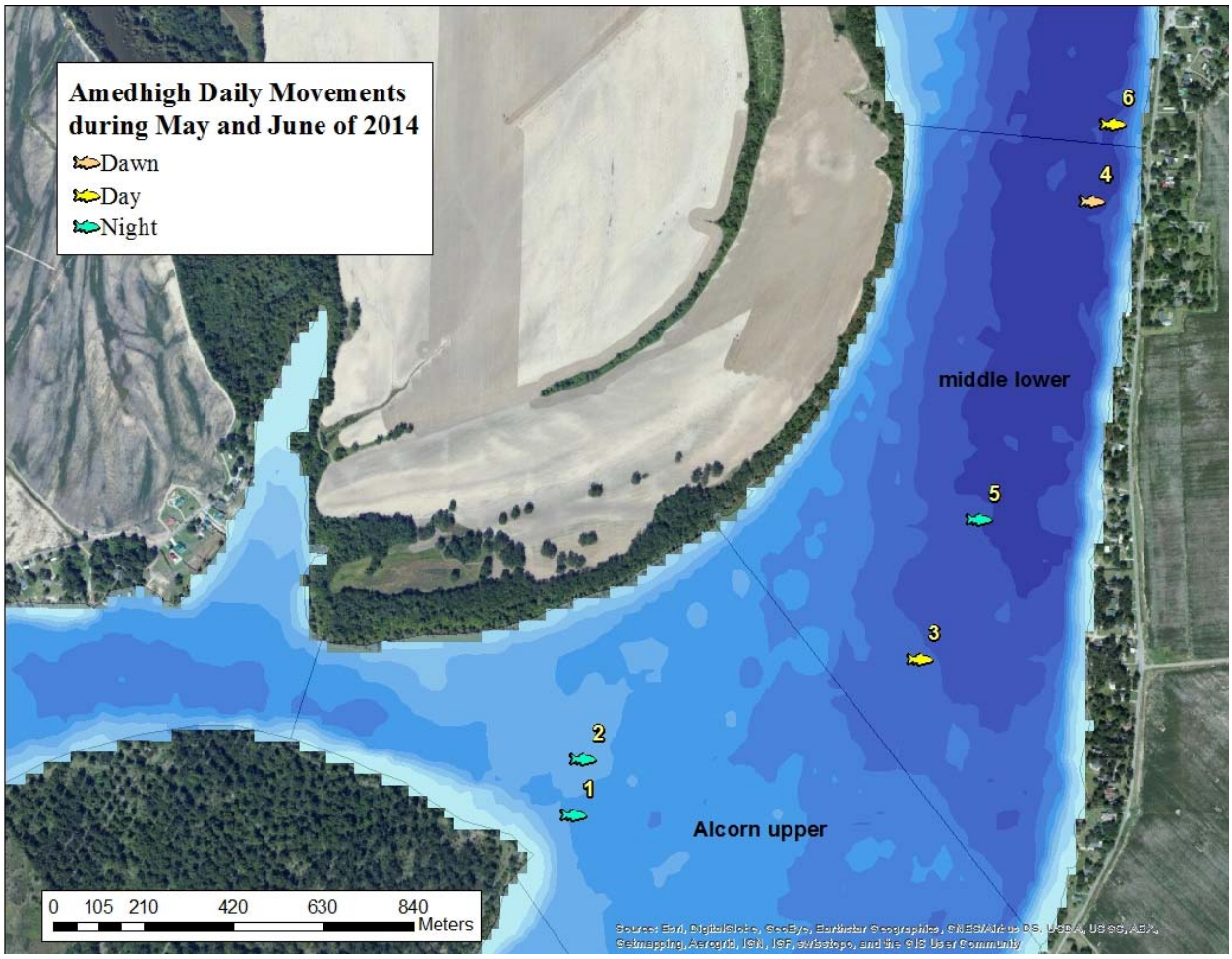

Figure 76. Daily movements of Amedhigh in May and June, 2014

“ichthyometer” remains a permanent fixture on the bottom of Moon Lake. No depth or temperature data was available. The first waypoint taken on Speedo2 was located in the lower middle lake section over a lake depth of 8.2 meters (Table 31). On September 17 Speedo2 entered Alcorn left on the west side of Alcorn Island. It was found over a depth of 5.12 meters. It swam south for 1.18 kilometers over a three hour period from 1637 to 1933 (Figure 77 waypoints 2 - 5). On September 20 Speedo2 was located seven times from 1534 to 1920 as it moved slowly south from middle lower into Alcorn upper (Figure 77 waypoints 17 - 23). Speedo2 was found in the same general area the following morning. It was located twice in Alcorn upper at 0752 and 0808 hours.

Habitat use of paddlefish based on depth, diel period, and season

Two measures of habitat use were used in this study: the depth of the lake taken at each paddlefish location and the depth of the fish as recorded by archival tags. All 526 locations were used in calculations of habitat use based on lake depth. Of the 526 plots of fish locations, only 147 locations had fish depth data. These included seven of the eleven fish from February (Ahti, Brizo, Ceto, Cymopoleia, Lir, Poseidon, and Tialoc) and one fish from May (Speedo).

During the winter, 84% of all fish were located over water 6 meters or deeper (Figure 78) with 90% of the fish located in the north upper, middle upper, and middle lower lake sections. Only 6% of fish were located in the north upper while only roughly 4% were located in Alcorn upper (Figure 79). Only one was located in Alcorn left. No fish during the winter were located in the lower three sections of the lake (Alcorn right, Alcorn lower, and south tip). Seasonal surface temperatures varied by lake section. The warmer surface temperatures during February were in the north upper (9.02°C) and Alcorn left lake sections (8.5°C). The coolest surface temperatures were in Alcorn upper (2.4°C) and middle lower (3.5°C). The average depth of the seven archived

Table 31. Waypoint information for Speedo2 in fall of 2014

Month - Day	Map ID	Time	Paddlefish ID	Lake Section	Lake Depth (m)
Sep-10	1	15:53:00	SPEEDO2	Middle_Lower	--
Sep-17	2	16:37:00	SPEEDO2	Alcorn_Left	--
Sep-17	3	16:46:00	SPEEDO2	Alcorn_Left	--
Sep-17	4	16:53:00	SPEEDO2	Alcorn_Left	--
Sep-17	5	16:55:00	SPEEDO2	Alcorn_Left	--
Sep-17	6	16:59:00	SPEEDO2	Alcorn_Left	--
Sep-17	7	17:05:00	SPEEDO2	Alcorn_Left	--
Sep-17	8	17:14:00	SPEEDO2	Alcorn_Left	--
Sep-17	9	17:44:00	SPEEDO2	Alcorn_Left	--
Sep-17	10	18:38:00	SPEEDO2	Alcorn_Left	--
Sep-17	11	18:50:00	SPEEDO2	Alcorn_Left	--
Sep-17	12	19:03:00	SPEEDO2	Alcorn_Left	--
Sep-17	13	19:09:00	SPEEDO2	Alcorn_Left	--
Sep-17	14	19:19:00	SPEEDO2	Alcorn_Left	--
Sep-17	15	19:33:00	SPEEDO2	Alcorn_Left	--
Sep-20	16	15:34:00	SPEEDO2	Middle_Lower	--
Sep-20	17	15:56:00	SPEEDO2	Middle_Lower	--
Sep-20	18	16:46:00	SPEEDO2	Middle_Lower	--
Sep-20	19	17:03:00	SPEEDO2	Middle_Lower	--
Sep-20	20	17:39:00	SPEEDO2	Middle_Lower	--
Sep-20	21	18:21:00	SPEEDO2	Middle_Lower	--
Sep-20	22	18:48:00	SPEEDO2	Alcorn_Upper	--
Sep-20	23	19:22:00	SPEEDO2	Alcorn_Upper	--
Sep-21	24	07:52:00	SPEEDO2	Alcorn_Upper	--
Sep-21	25	08:08:00	SPEEDO2	Alcorn_Upper	--

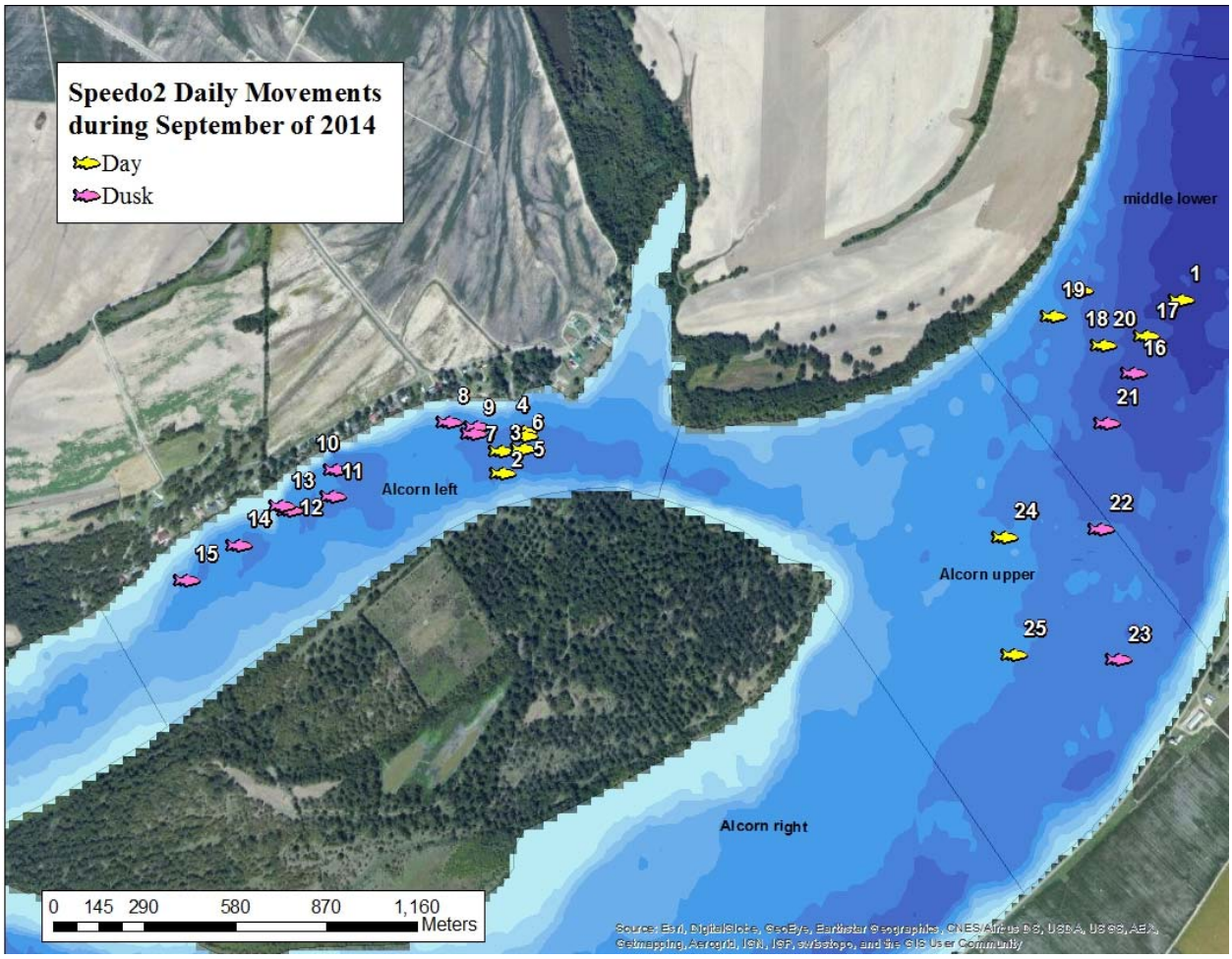

Figure 77. Speedo2 fall movements on September 17, 2014

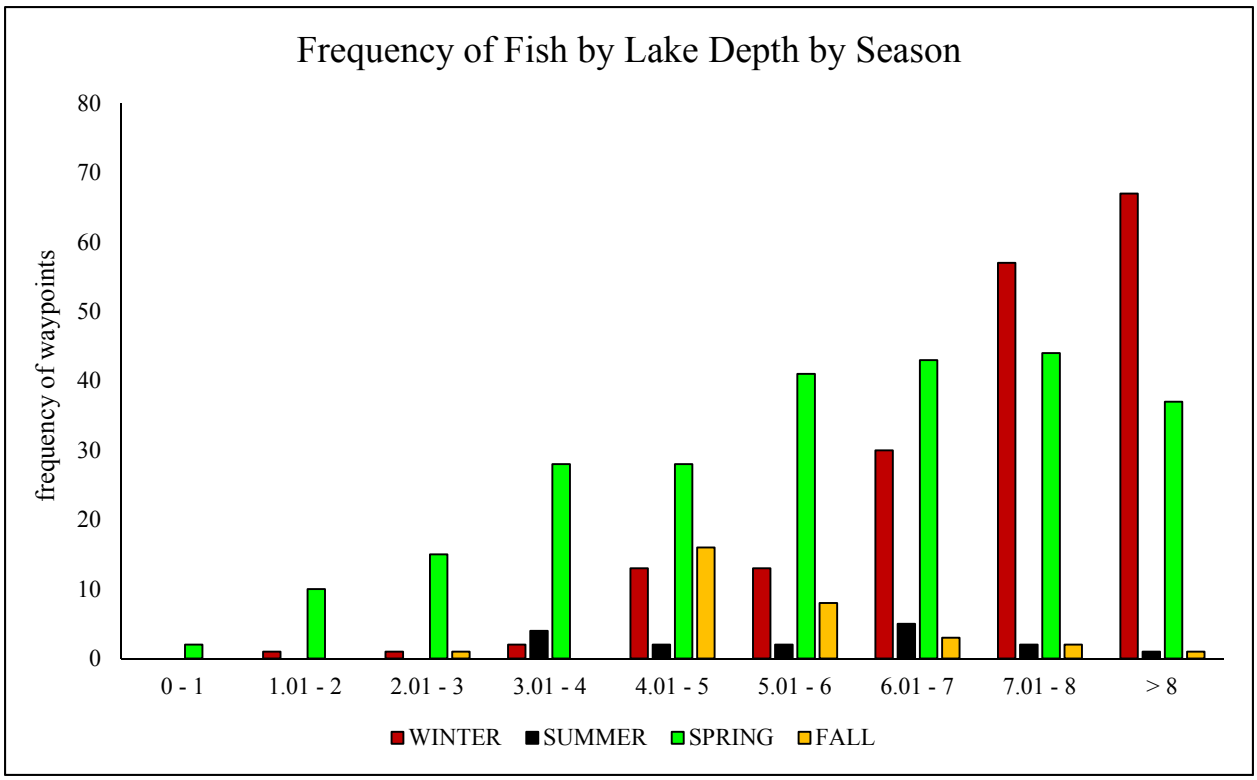

Figure 78. Frequency distribution of number of waypoints at lake depth by season

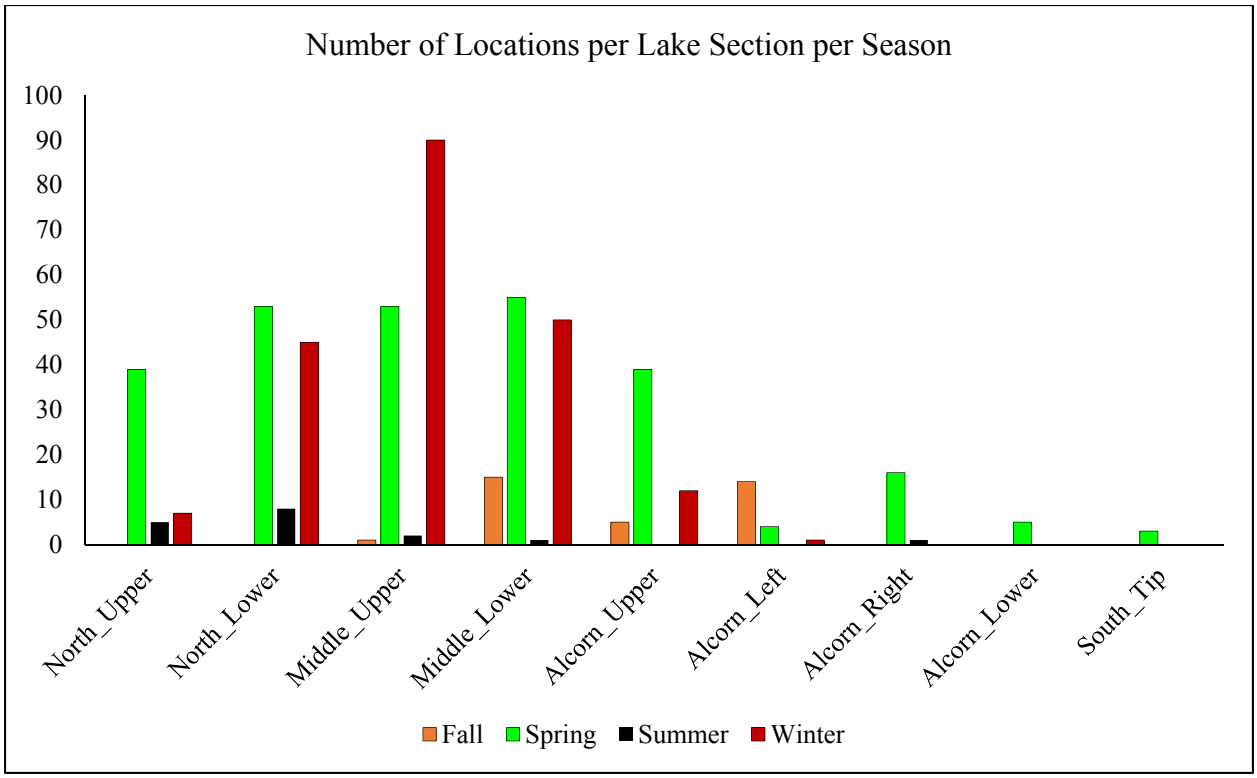

Figure 79. Frequency of fish locations per lake section

fish was 4.84 meters with a minimum depth of 0.51 meters and a maximum depth of 9.7 (Figure 80). Average fish temperature over February was 5.79°C with a minimum of 2.42°C and a maximum of 11.58°C. Fifty-four percent of the daytime locations were in the middle upper and middle lower lake areas (Figure 81). Fish with archival tags that were in these areas were generally at depths greater than 6 meters (Figure 82). Eighty-two percent of the locations at dusk were taken in waters greater than 7 meters.

In the spring fish locations were spread out over shallower waters with only 50% of the locations now located over waters of 6 meters depth or deeper (Figure 78). Twenty-two percent of the fish were located in water less than 4 meters in depth. Nearly seventy-five percent of locations were spread out over the upper four sections (56%) of the lake. Twenty-five percent of the excursions were into the lower half of the lake. Surface temperatures warmed considerably in the spring and were relatively uniform from north to south. Higher temperatures were in Alcorn upper and Alcorn left at around 19.0°C. Lowest temperature was in north upper (15.69°C).

Speedo was the only fish to have depth and temperature data recorded during the spring. The average depth in May was 4.6 meters with a range of depths from the surface down to 10.2 meters. The average temperature was 21.5°C with a minimum and maximum of 18.42°C and 24.71°C, respectively. In the spring more locations were recorded in less than three meters more often in the evening and night than at any other time (Figure 83), but paddlefish seemed to begin to move freely regardless of the diel periods when the temperatures begin to warm (Figure 84).

Fall and summer saw a drop-off in fish locations as many fish had left the lake in mid-to-late summer. Of the fish from 2013 only *Anapos* and *Amphitrite* remained into the summer before leaving the lake on June 11 and June 21, respectively. In 2014, two fish (Amedhigh and Alittlehigh) were tagged on May 3. Amedhigh was located twice on the 16th of June traveling

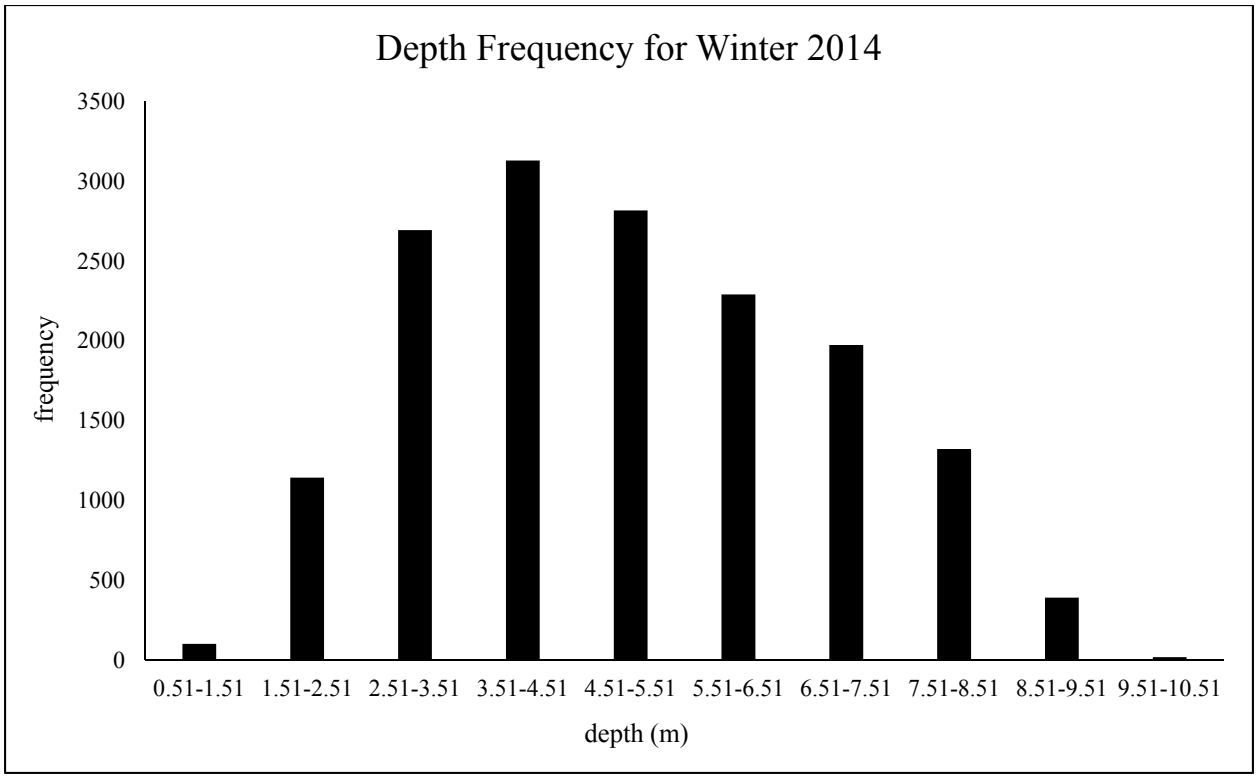

Figure 80: Average depth of fish with archival tags from February of 2014

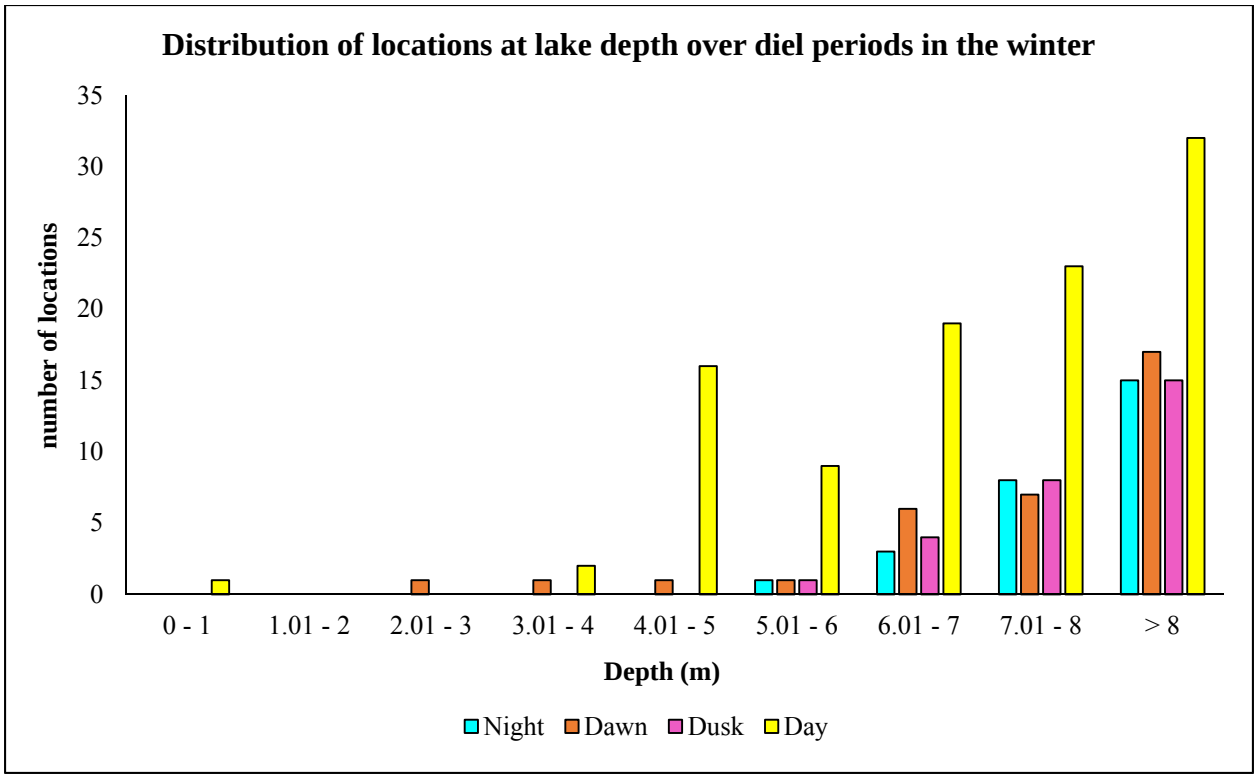

Figure 81. Frequency of locations at lake depths for winter diel periods

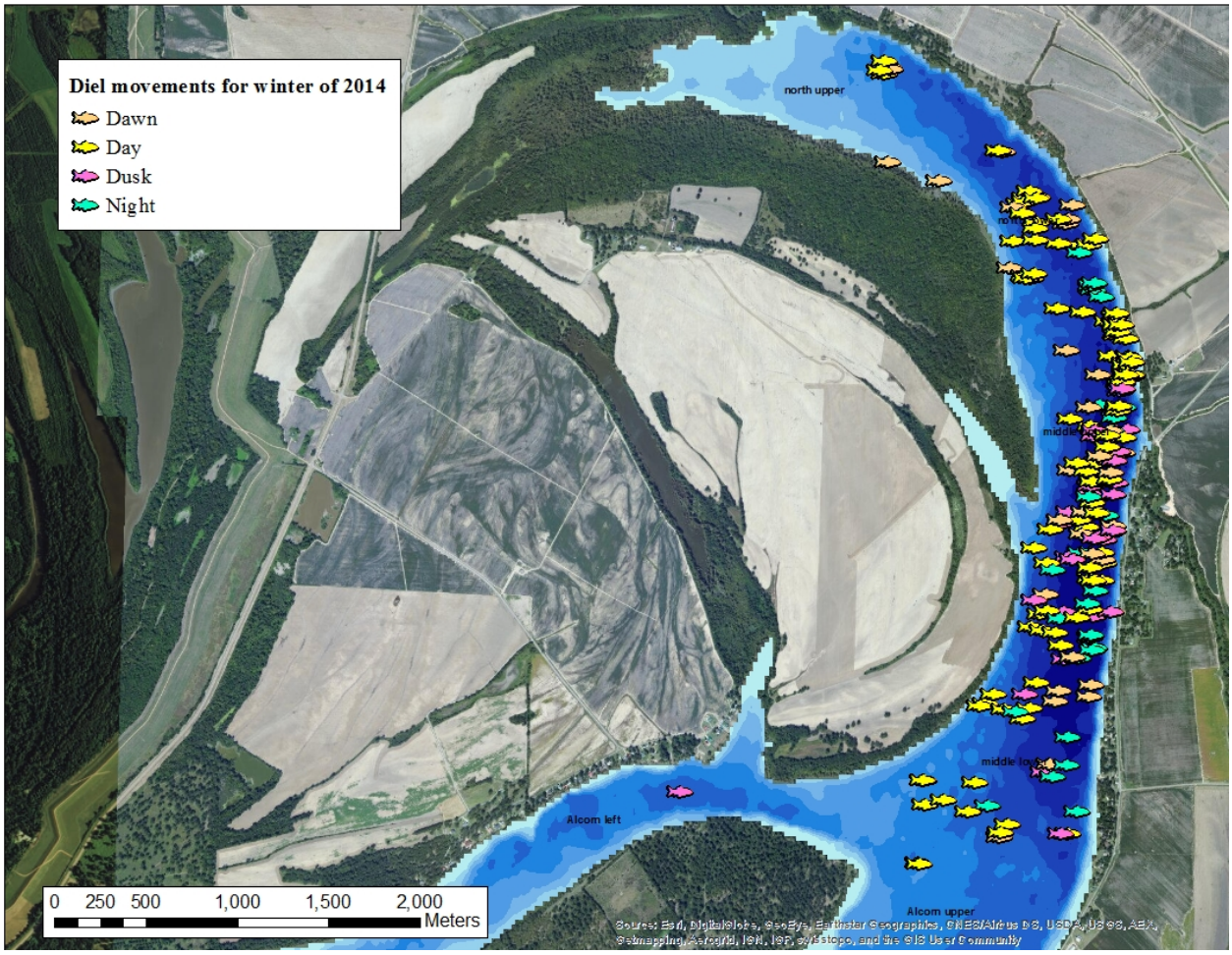

Figure 82. Diel movement for winter of 2014

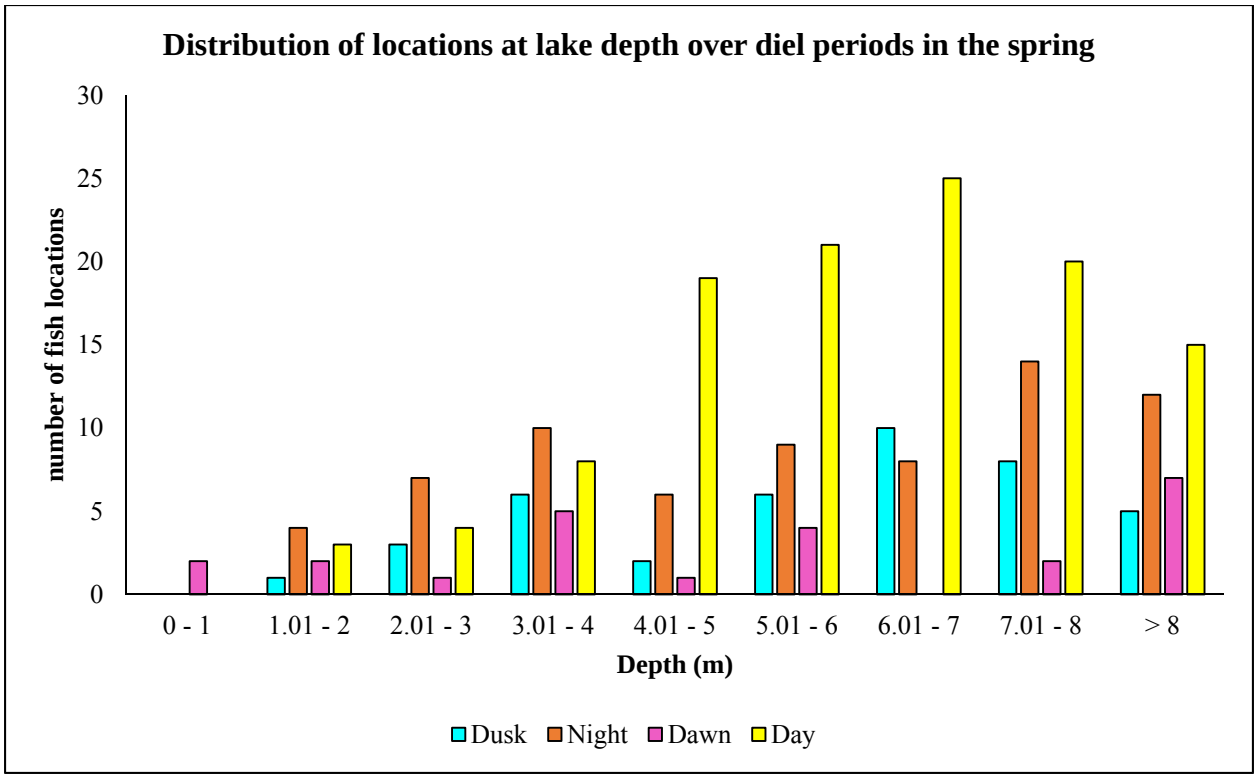

Figure 83. Frequency of locations at lake depths for spring diel periods

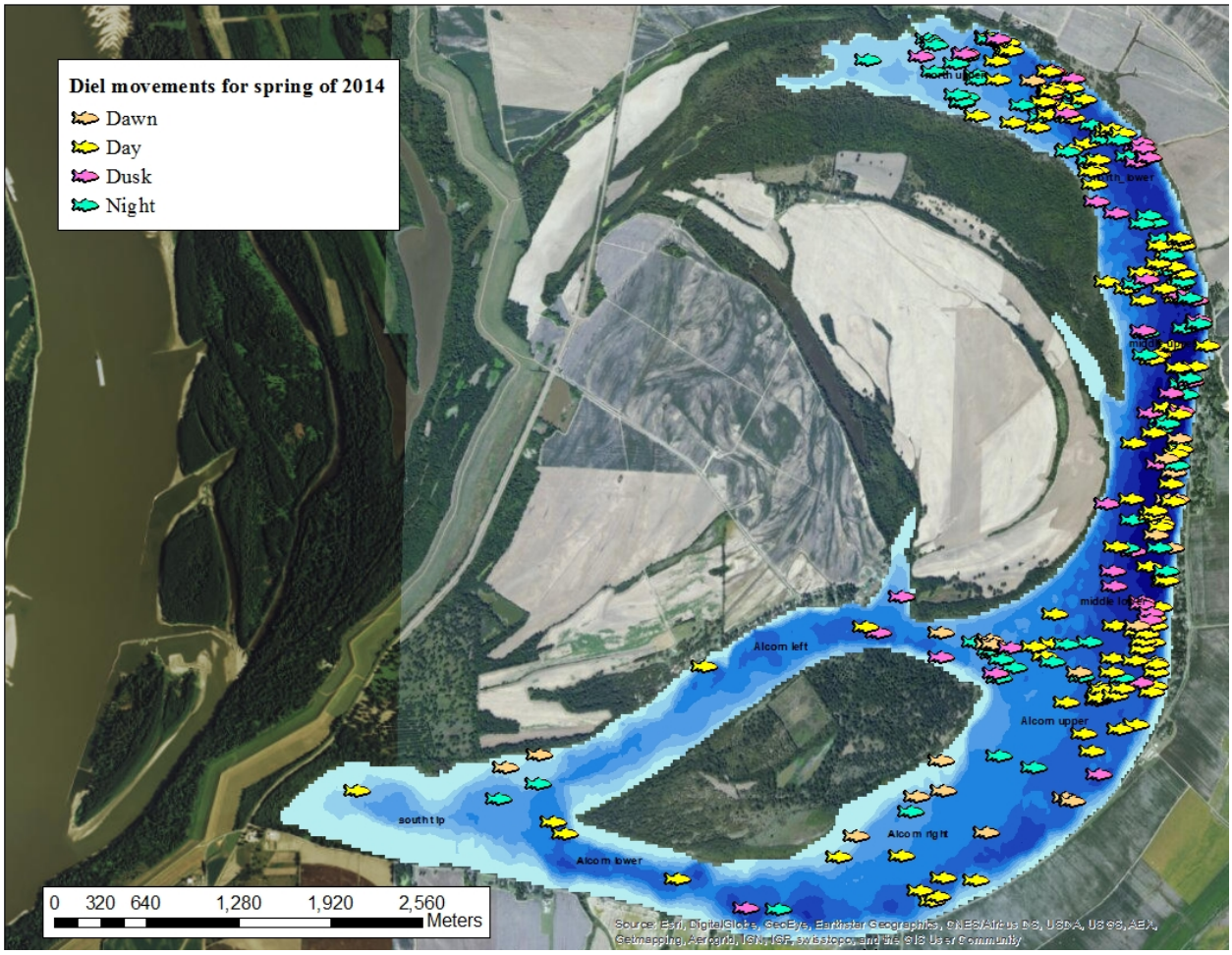

Figure 84. Diel movement for spring of 2014

north between Alcorn right and middle lower from 0943 to 1357 hours in the afternoon, but wasn't located after this date. Both fish were on occasion located together on June 16, but only Alittlehigh stayed until July 21. The majority of the summer locations were in the north part of the lake (89%) at lake depths deeper than 3 meters (Figure 85).

Two fish were tracked during the fall; one in 2012 and the other in 2014. *Copeia* was captured on November 7, 2012 and was located ten times in the fall. This paddlefish was located a single time in Alcorn upper on November 17 over a depth of 4.5 meters. On November 30 *Copeia* made a short, but fast trip north moving nearly 2 kilometers in 16 minutes at a velocity of 213 centimeters per second. He returned to the original location after only 28 minutes and spent the next hour on the west shore of middle lower. It was in shallow water ranging from 4.3 to 5.6 meters in depth. The distributions of locations over lake depth are shown in Figure 86.

Rostrum Area and Shape

The rostrum areas (cm^2), fish weights (kg), rostrum shape index numbers, and the ratio of rostrum area (cm^2) to fish mass (kg) are listed in Table 21. There was a slight increase in calories per cubic meter with increasing rostrum area ($R^2 = 0.06$) (Figure 87, Figure 88), but the calories per cubic meter were highly variable among sites. The number of zooplankton samples burned to calculate caloric value for each fish locality are shown in Figure 89. There was not a linear relationship between average density per cubic meter and rostrum area ($R^2 = 0.01$) (Figure 90, Figure 91). The number of zooplankton samples counted to calculate average density for each fish locality are shown Figure 92. The number of sites sampled per fish, the random locality to calculate the calories per cubic meter, and the average densities during the spring and winter, 2014 are listed in Table 32 and Table 33. The two fish with damaged rostrums were Alpheus and Tialoc. Alpheus had significant damage to its rostrum (Figure 51) and the lowest rostrum area of

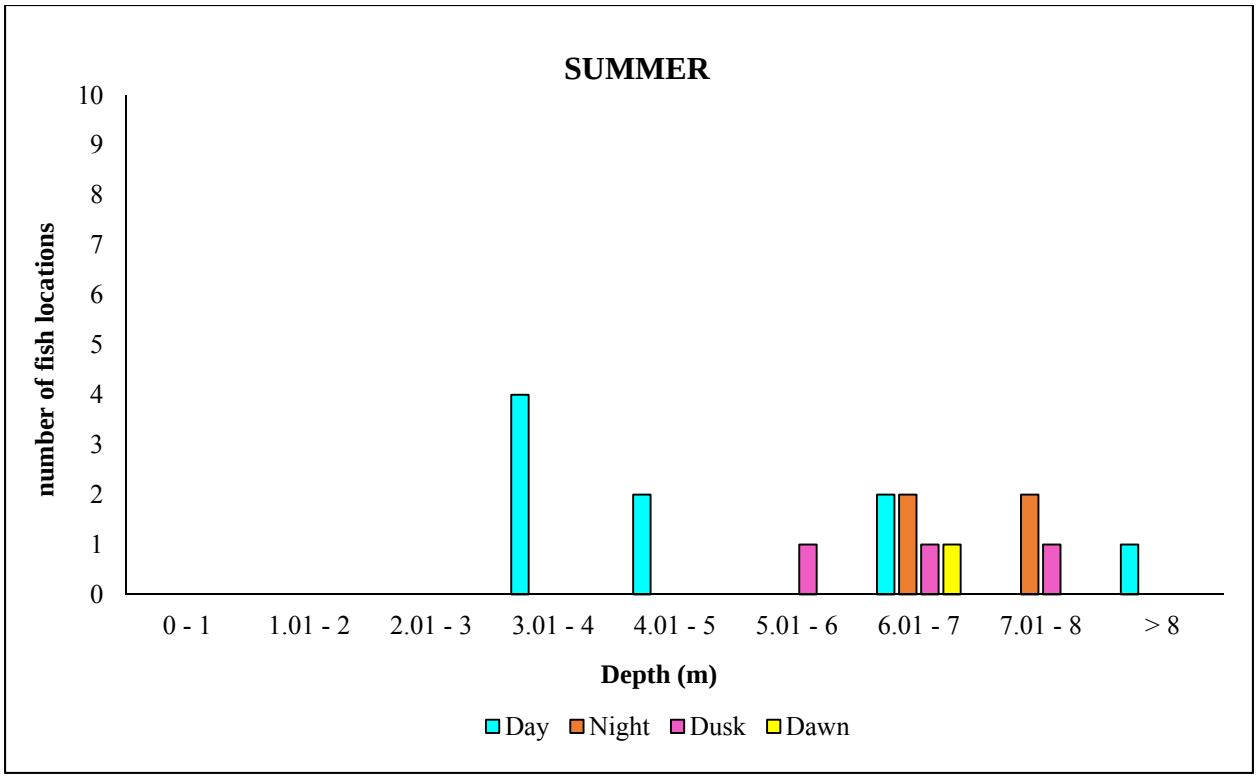

Figure 85. Frequency of locations at lake depths for summer diel periods

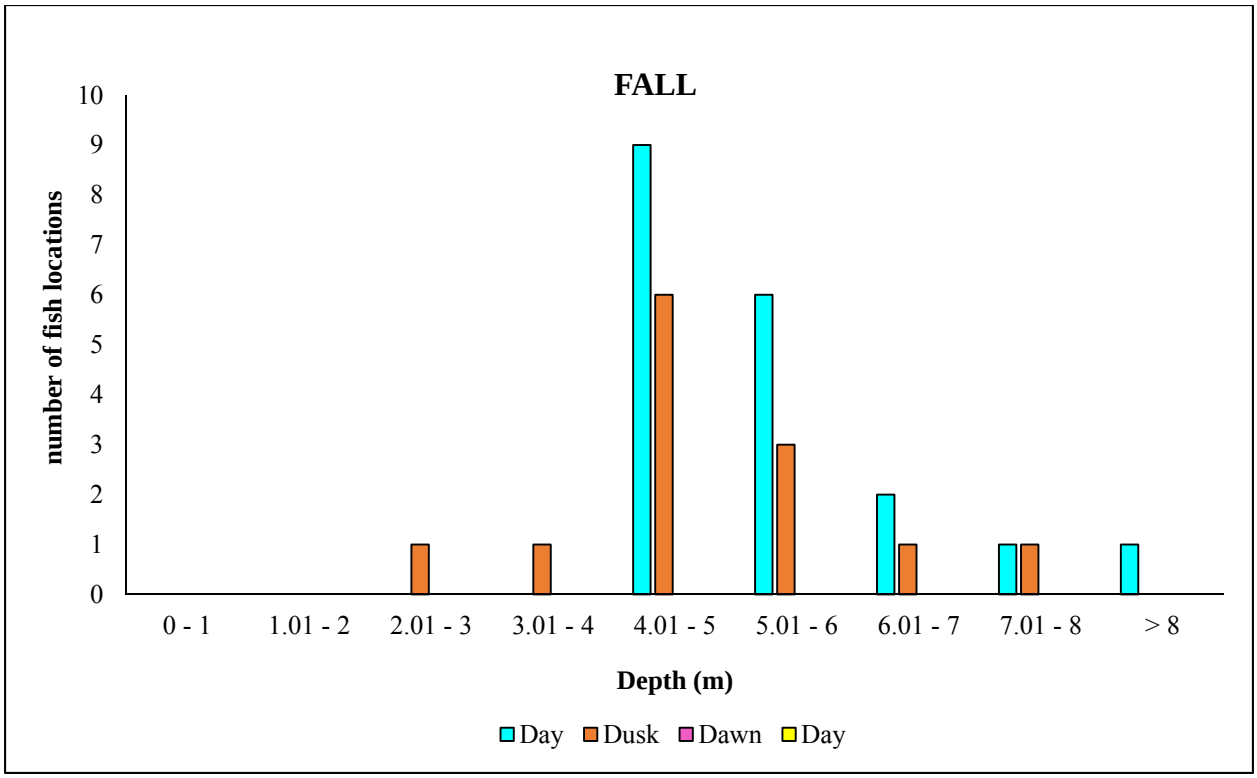

Figure 86. Frequency of locations at lake depths for fall diel periods

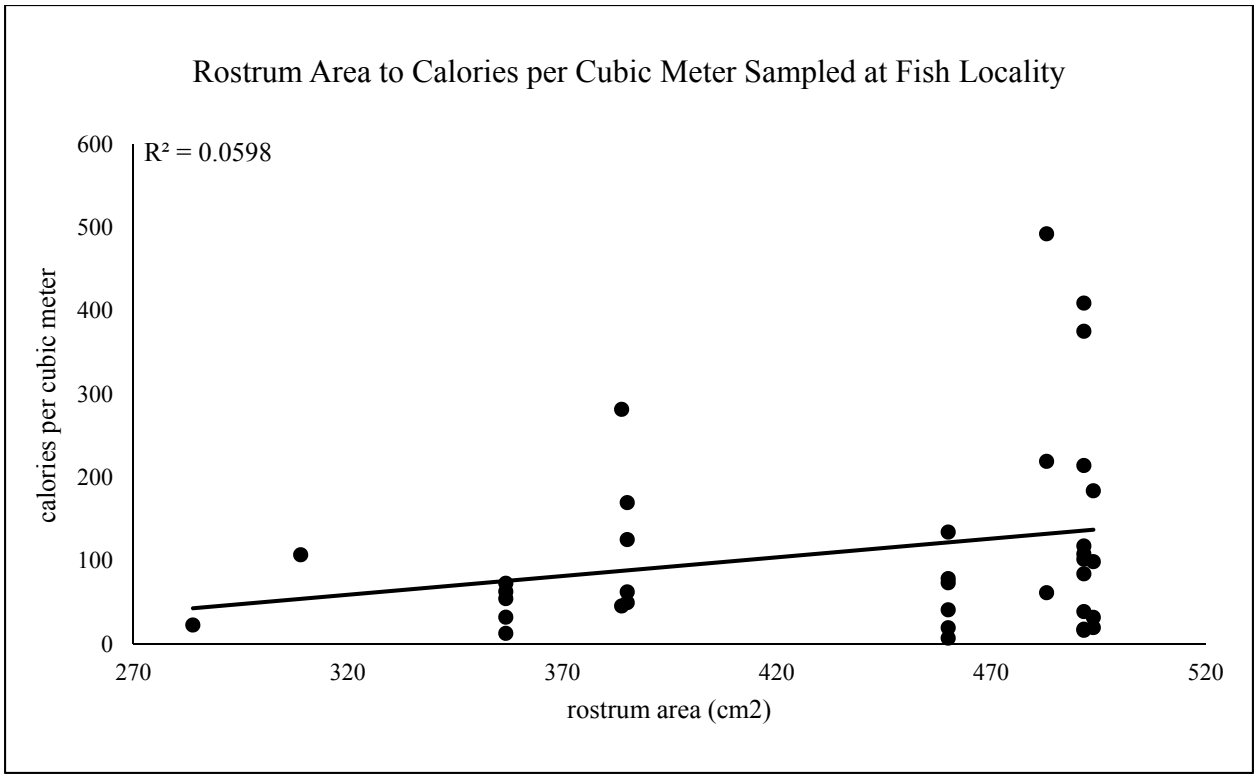

Figure 87. Relationship between rostrum area (cm^2) and calories per cubic meter

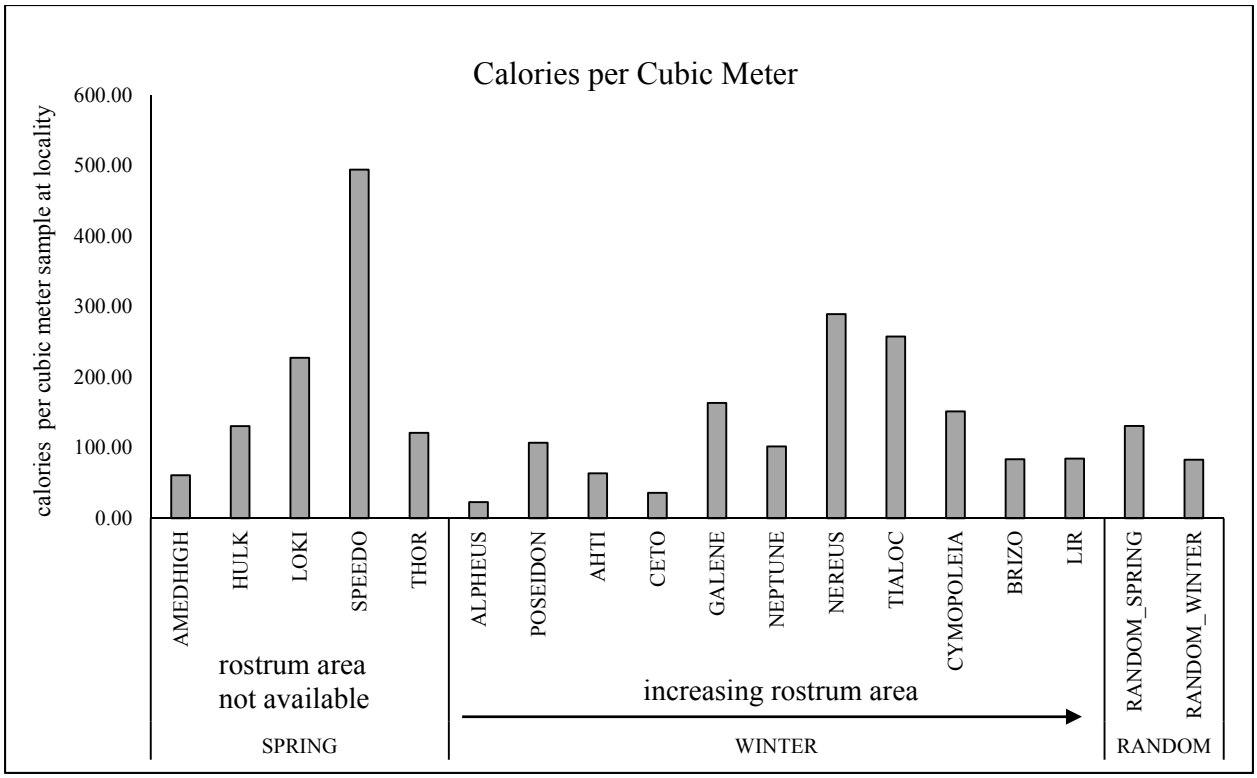

Figure 88. The average calories per cubic meter per fish and random locality for the spring and winter of 2014

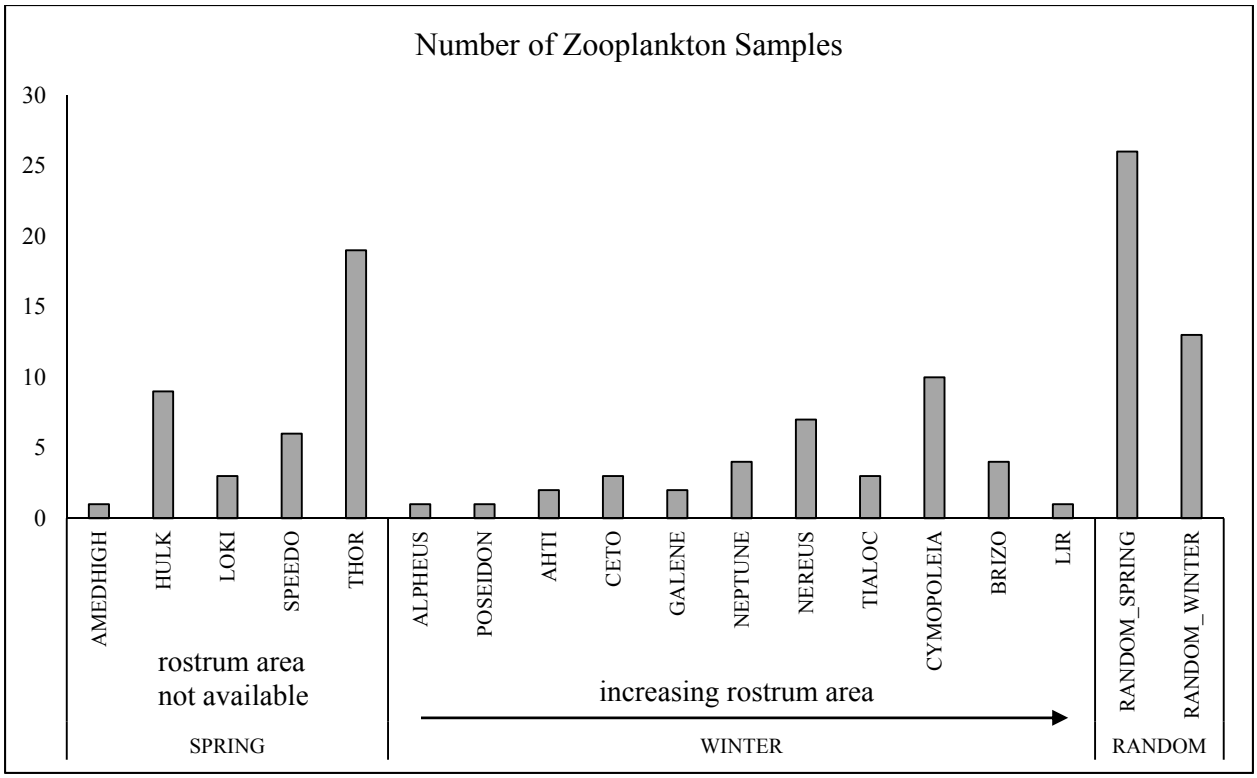

Figure 89. The number of zooplankton samples taken per fish and random locality to calculate calories per cubic meter during the spring and winter of 2014

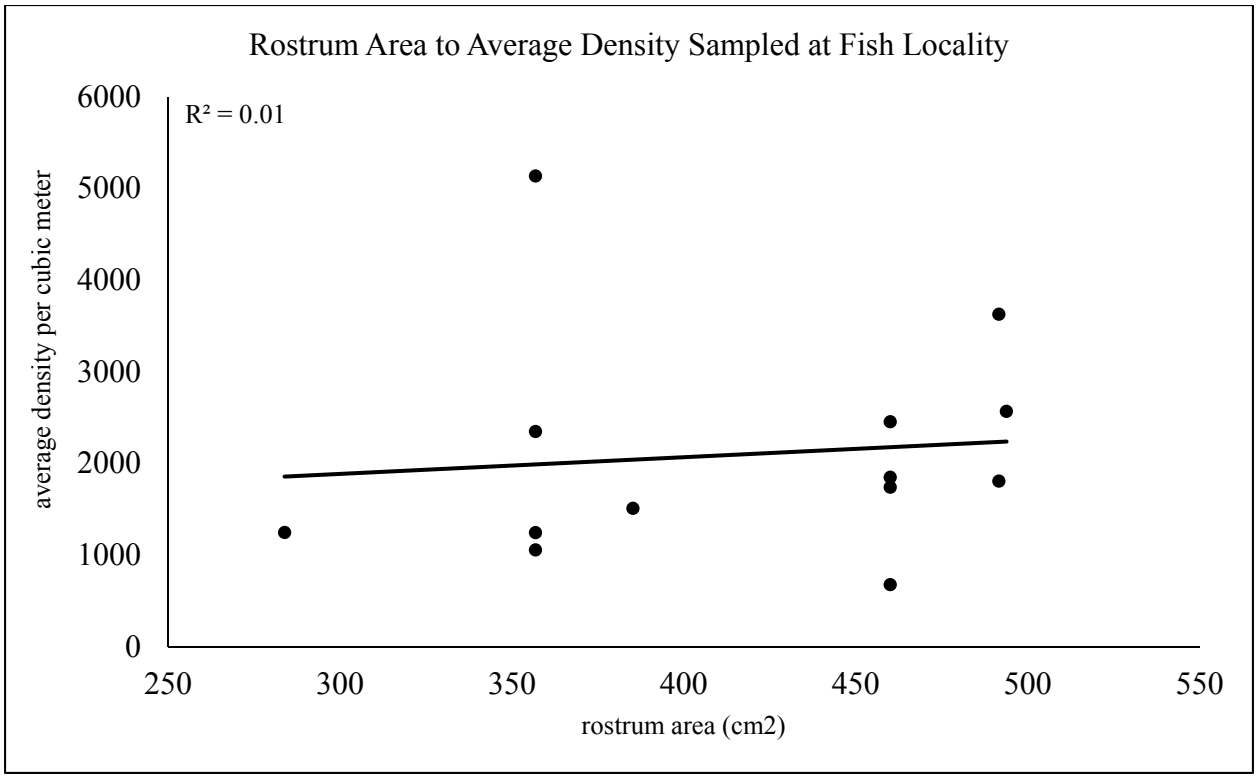

Figure 90. Relationship between rostrum area (cm^2) and average density per cubic meter

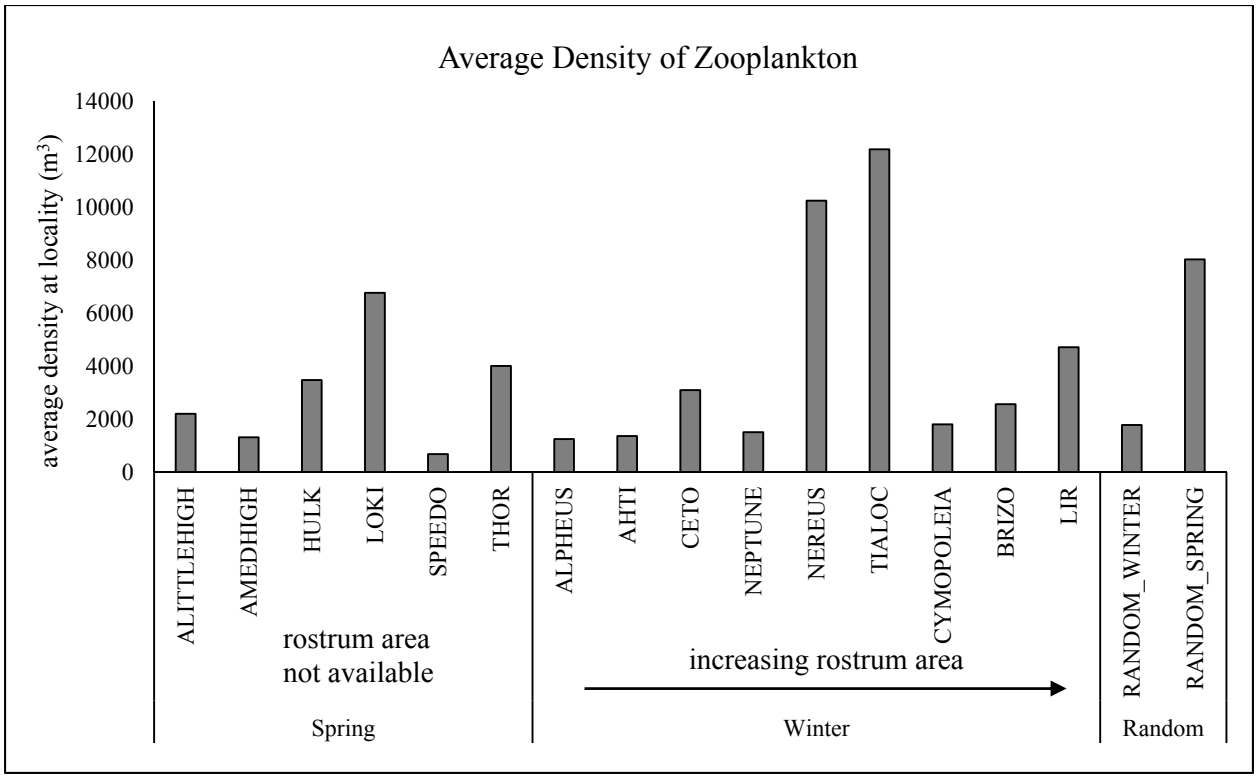

Figure 91. The average density per cubic meter per fish and random locality for the spring and winter of 2014

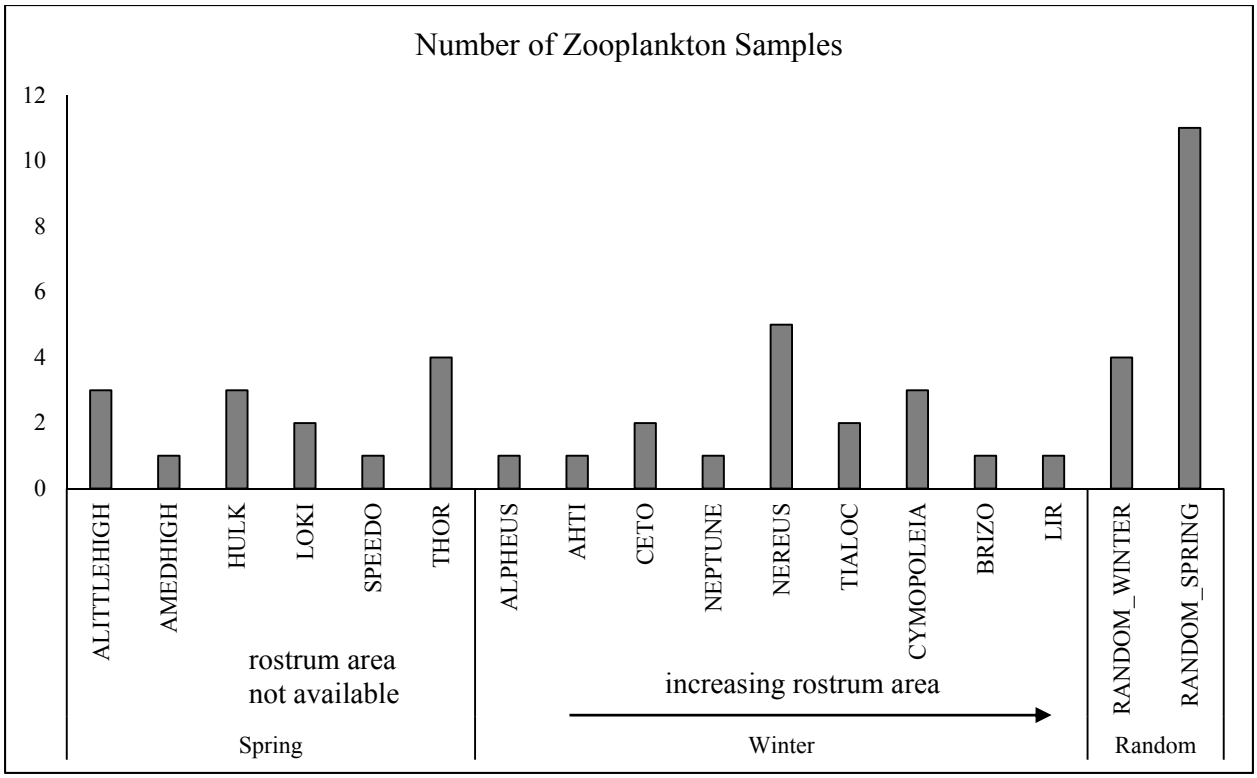

Figure 92. The number of zooplankton samples taken per fish and random locality to calculate average density during the spring and winter of 2014

Table 32. Rostrum Area, Average Calories per Cubic Meter from Zooplankton Samples, and the Number of Zooplankton Samples taken per fish and random locality

Season	Paddlefish ID	Rostrum Area (cm^2)	Calories (m3)	No. of Samples
Spring	AMEDHIGH	--	61.15	1
	HULK	--	130.80	9
	LOKI	--	227.59	3
	SPEEDO	--	494.47	6
	THOR	--	121.20	19
Winter	ALPHEUS	283.86	22.85	1
	POSEIDON	309	107.18	1
	AHTI	356.86	63.75	2
	CETO	356.86	36.15	3
	GALENE	383.84	163.70	2
	NEPTUNE	385.17	101.92	4
	NEREUS	460	289.55	7
	TIALOC	482.94	257.76	3
	CYMOPOLEIA	491.61	151.47	10
	BRIZO	493.82	83.76	4
	LIR	--	84.62	1
Random	SPRING	--	130.88	26
	WINTER	--	83.02	13

Table 33. Rostrum Area, Average Density per Cubic Meter from Zooplankton Samples, and the Number of Zooplankton Samples taken per fish and random locality

Season	Paddlefish ID	Rostrum Area (cm2)	Avg. Density (no./m3)	No. of Samples	Weight (kg)
Spring	ALITTLEHIGH	0	2204.06	3	0.00
	AMEDHIGH	0	1309.58	1	0.00
	HULK	0	3477.52	3	0.00
	LOKI	0	6773.63	2	0.00
	SPEEDO	0	679.69	1	0.00
	THOR	0	4012.29	4	0.00
Winter	ALPHEUS	283.86	1245.46	1	26.42
	AHTI	356.86	1359.77	1	17.41
	CETO	356.86	3094.42	2	10.03
	NEPTUNE	385.17	1508.01	1	17.46
	NEREUS	460.00	10259.46	5	35.01
	TIALOC	482.94	12199.36	2	34.02
	CYMOPOLEIA	491.61	1805.19	3	19.59
	BRIZO	493.82	2565.91	1	15.82
	LIR		4715.50	1	0.00
Random	SPRING	0	1780.76	4	0.00
	WINTER	0	8035.96	11	0.00

the paddlefish measured. Tialoc, on the other hand, had the second largest rostrum area of the group despite the damaged area (482.94 cm^2). Of the entire group Alpheus had the lowest average calories per cubic meter (22.8 cal/m^3) per sample location. Surprisingly, Tialoc had the second highest calorie count (257.76 cal/m^3) (Figure 51).

Meteorology and Movement

Compiled meteorological data was compared with fish movements during February, 2014 to evaluate the effect of wind direction and speed (km/h) on movement of paddlefish. Ten paddlefish (Ahti, Alpheus, Brizo, Ceto, Cymopoleia, Galene, Lir, Neptune, Nereus, Poseidon, and Tialoc) were located on eight separate days (February 1, 8, 9, 14, 15, 16, 17, and 23) during 2014. The following is a detailed account of their movements in relation to local zooplankton availability, temperature, wind direction, and wind speed and to a lesser extent the effect of relative humidity and barometric pressure.

On February 1, all ten fish were located over deep water in the middle three sections of Moon Lake (north lower, middle upper, middle lower). These fish were in this area from 0224 to 2358 hours (Figure 93). Nine zooplankton tows were taken over the course of the day. The average calories per cubic meter in north lower and middle lower were around 1,672 (n=2). The average was lower in middle upper at 256 (n=7). The average fish depth in north lower was 5.61 meters at an average temperature of 4.01°C. Fish in middle upper were swimming slightly deeper at an average of about 6.92 meters at 3.5°C. The wind was from the west at an average of 8.62 kilometers per hour. It was fairly consistent from 0300 to 0700 hours. The wind from the north/northeast in the afternoon was consistent but negligible, averaging less than a kilometer per hour (Figure 94). Data before and after were not taken. The average temperature was 15°C with an average relative humidity of 66.31% and an average barometric pressure of 1014.77. The

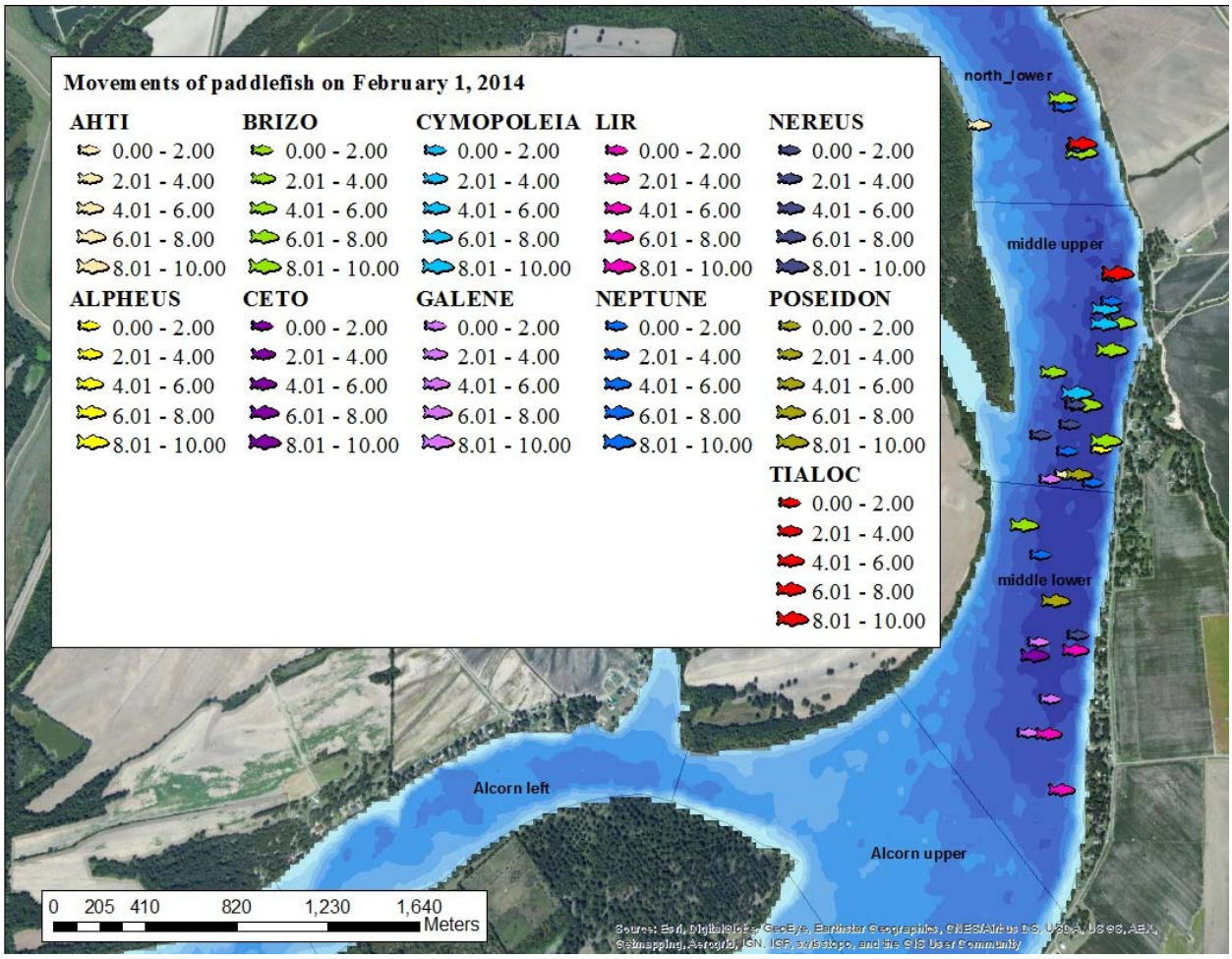

Figure 93. Movement with Weather Patterns on February 1, 2014

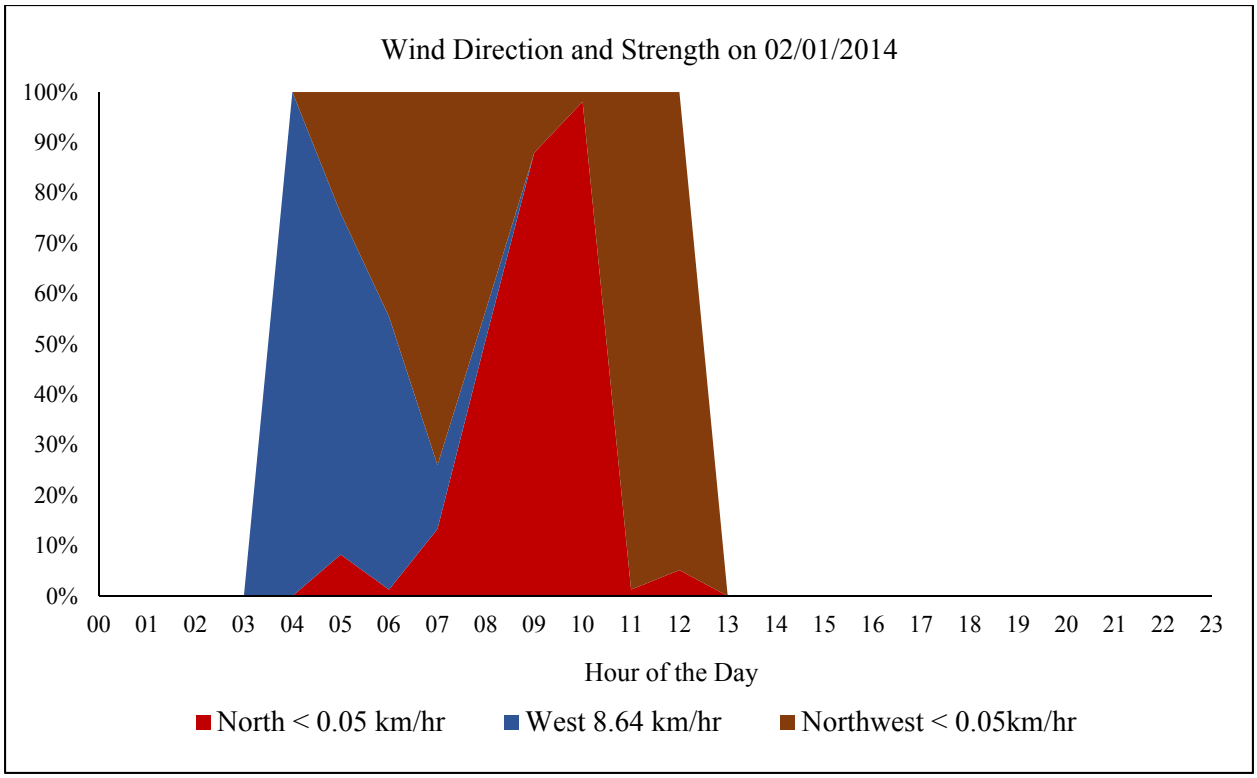

Figure 94. Wind Direction and Strength on February 1, 2014

hourly depth and temperature each paddlefish was swimming is listed in Table 34. The lake section and the depth as a percentage of the water column are also provided.

On February 8, 2014 six of the ten fish were located on the east side of the lake between the borders of middle upper and middle lower (Figure 95). The paddlefish ranged in depth between 5 and 8 meters at temperatures between 2.15 to 4.6°C. Lir was the shallowest of the fish, swimming at roughly 5 meters and Tialoc (deformed rostrum) was swimming the deepest at a depth of 7.65 meters. Zooplankton concentration around 1515 hr. around the vicinity of Cymopoleia was 1,805 organisms per cubic meter or 1.8 org/L. The wind was consistent from the northwest at one kilometer per hour from 1500 to 2000 hours before subsiding altogether. The air temperature rose steadily (1.32 to 17.29°C) from 1500 hours to midnight. The relative humidity fell and the barometric pressure was around 1020 mmHg (Table 35).

On February 15, a front moved through that brought variable winds primarily from the south/southeast between 16.27 and 25.44 km/hr. The winds began to shift around 2000 hr. coming from the southwest at 6.72 km/h and shifted back around midnight (Figure 96). The majority of the fish were clustered in the center of middle upper (Figure 97). Nereus remained south of the group. Poseidon joined Ahti around midnight at the border between Alcorn upper and middle lower. Ahti's location just two hours prior was in north lower. This was a distance of 2.76 kilometers to the north. Poseidon was swimming at nearly 5 meters depth at a temperature of 2.29°C. Ahti was a bit shallower on average at 2.55 meters and 2.42°C. The bulk of the larger group was located in middle upper. Neptune and Nereus were the most active of this group swimming a half kilometer south of the others. The average density of zooplankton was a bit higher and may be the reason for the difference in location (1,144) and apparent activity. The concentrations in middle upper were around 500 organisms per cubic meter. The temperatures

Table 34. Movement, depths, and temperature of paddlefish on February 1 of 2014

Hour	Lake Section	Paddlefish ID	Avg. Fish Depth	Avg. Fish Temp	No. Locations	%Water Column
02	Middle upper	CYMOPOLEIA	6.64	3.24	1	0.82
03	Middle upper	CYMOPOLEIA	7.15	3.24	1	0.87
		NEREUS	0	0	1	0.00
04	Middle lower	GALENE	0	0	1	0.00
		LIR	4.07	3.24	2	0.64
		NEPTUNE	0	0	1	0.00
	Middle upper	AHTI	1.53	3.11	1	0.19
05	Middle lower	BRIZO	6.13	3.52	1	0.93
	Middle upper	ALPHEUS	0	0	1	0.00
		NEREUS	0	0	2	0.00
		POSEIDON	5.1	3.24	1	0.60
07	Middle lower	GALENE	0	0	1	0.00
		LIR	5.09	3.24	1	0.63
		POSEIDON	6.63	3.24	1	0.84
		NEPTUNE	0	0	1	0.00
	North lower	AHTI	2.55	3.38	1	0.94
08	Middle lower	CETO	6.12	3.38	1	0.82
		GALENE	0	0	1	0.00
		NEREUS	0	0	1	0.00
	Middle upper	ALPHEUS	0	0	1	0.00
		BRIZO	8.935	3.24	2	1.06
		NEPTUNE	0	0	1	0.00
15	Middle upper	NEPTUNE	0	0	1	0.00
	North lower	BRIZO	7.15	4.06	1	0.98
17	Middle upper	BRIZO	7.15	3.93	1	0.88
18	Middle upper	BRIZO	8.68	3.93	1	1.02
		NEPTUNE	0	0	1	0.00
		TIALOC	8.16	4.06	1	1.00
19	Middle upper	GALENE	0	0	1	0.00
20	Middle upper	CYMOPOLEIA	8.17	4.06	1	0.98
22	North lower	AHTI	2.55	4.06	1	0.34
		BRIZO	8.68	4.34	1	1.14
		NEPTUNE	0	0	1	0.00
		TIALOC	7.14	4.2	1	0.95
23	North lower	NEPTUNE	0	0	1	0.00
	Grand Total		3.49	2.01	39	0.47

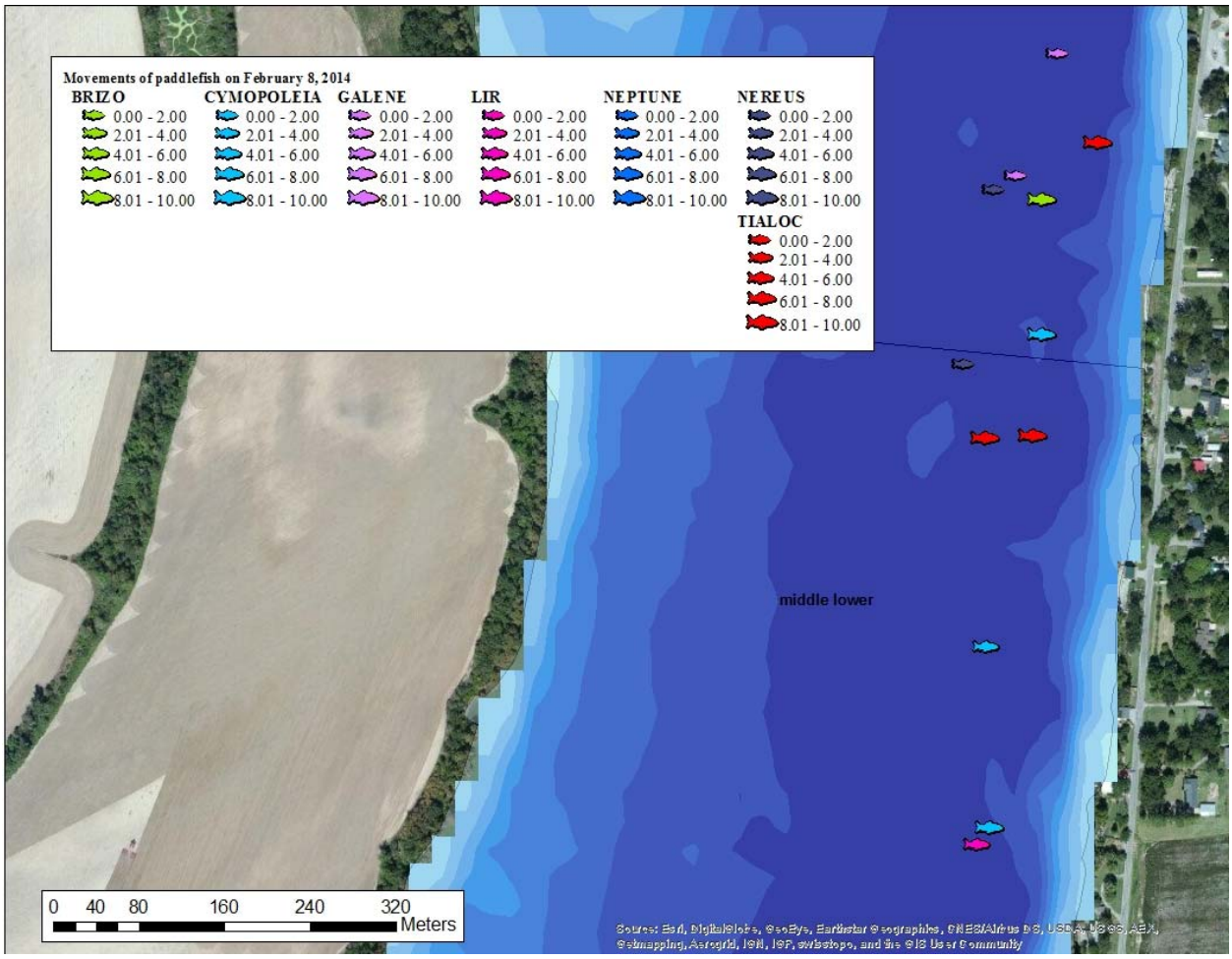

Figure 95. Movement with Weather Patterns on February 8, 2014

Table 35. Weather data on February 8 of 2014

Hour	Wind Speed km/h	T°C	%RH	BP mmHg
15	2.42	1.32	88.69	1021.85
16	1.66	1.10	89.78	1022.39
17	1.15	1.07	90.32	1022.44
18	1.57	0.69	93.15	1021.70
19	0.64	0.74	93.18	1021.50
20	1.77	0.84	93.08	1021.03
21	0.00	3.38	83.62	1020.22
22	0.00	8.09	86.79	1019.74
23	0.00	17.29	58.38	1020.20

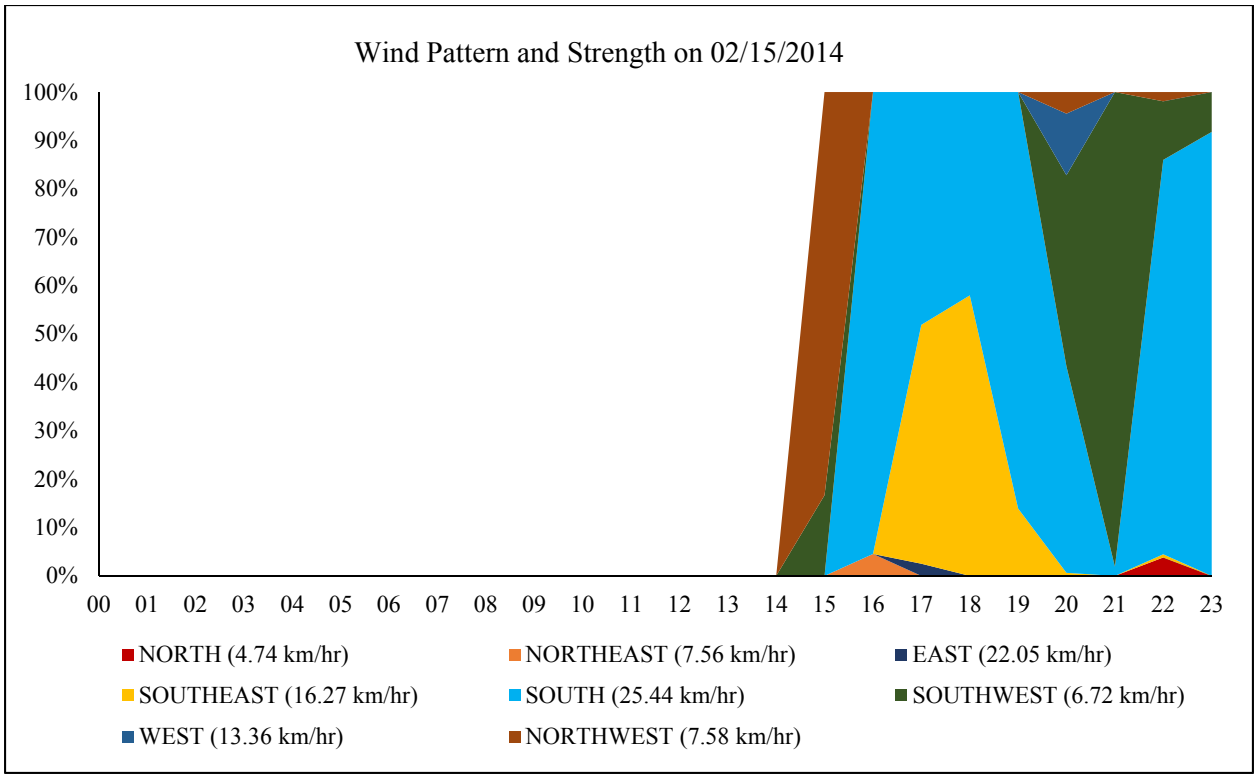

Figure 96. Wind Direction and Strength on February 15, 2014

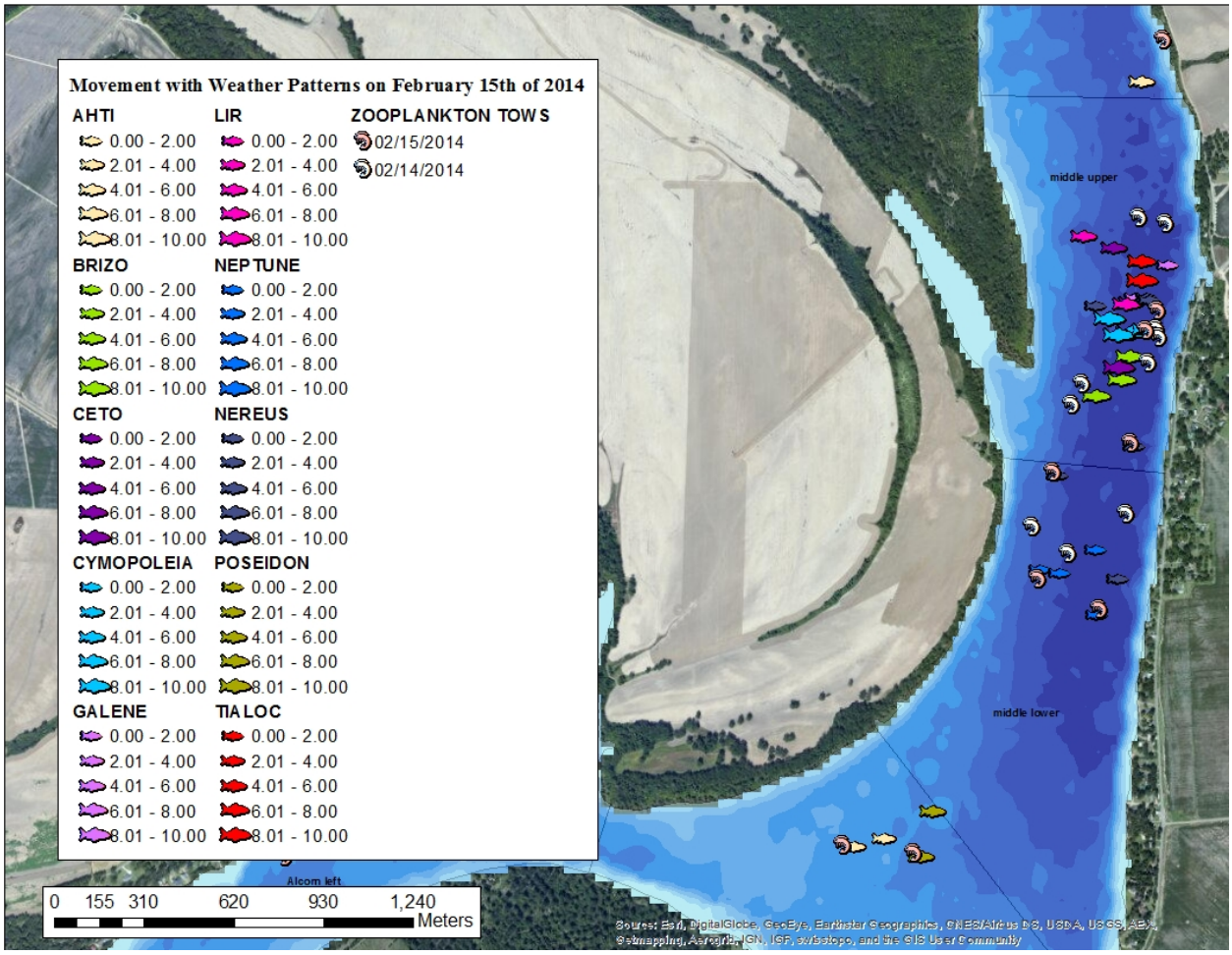

Figure 97. Movement with Weather Patterns on February 15, 2014

over this track declined as the hours grew later ranging from 20.7°C at 1500 hr. to 2.82°C around 2300 hr. The relative humidity rose along with the afternoon and evening rains, but barometric pressure did not change after the rain began (1019 mmHg). The location, average temperature and depth of each paddlefish over this tracking period are listed in Table 36.

The winds changed from southerly to northerly overnight. On February 16 wind direction was from the north/northeast at 35.23 km/h from 0900 to 1500 hours (Figure 98). Five fish were located from the middle upper south to Alcorn upper (Figure 99). Nereus was located in the upper northeast corner of middle upper at 1026. The average zooplankton density was relatively high for the winter at 1,848 org/m^3 (Table 37). The caloric value was 78.58 calories per cubic meter. Further southwest, on the border between middle upper and middle lower Lir was recorded swimming at an average depth of 5.6 meters at 2.7°C. This was about 86% of the water depth in the area. The zooplankton average density was high at 4,716 organisms per cubic meter. The caloric availability was 84.62 (cal/m^3). Ceto was located just 17 minutes after Lir, and was less than a half of a kilometer to the south/southwest. The fish was swimming near the bottom (93%) at a depth of 6.12 meters and a temperature of 2.83°C. Again, the caloric concentration was extremely high with an average density of 5,135 and 63.07 calories per cubic meter. Further south (1.02 km) Poseidon and Ahti were located also active in zooplankton rich waters. Their depths were 3.06 and 3.57 meters, respectively and the area temperature was 2.8°C. The zooplankton density was 2,347 org/m^3 at a caloric value of 83.5 calories per cubic meter. The locations, depths, and temperature of fish located on February 16 are located in Table 38.

Toward the south part of Alcorn Island the zooplankton concentrations from random samples were quite high. In Alcorn in the narrow channel the zooplankton concentrations which were 3,355 organisms per cubic meter, but more impressive is the caloric value of these

Table 36. Movement, depths, and temperature of paddlefish on February 15, 2014

Hour	Lake Section	Paddlefish ID	Avg. Fish Depth	Avg. Fish Temp	No. Locations	%Water Column
09	Middle upper	NEREUS	--	--	1	--
10	Middle lower	NEPTUNE	--	--	1	--
	Middle upper	BRIZO	7.66	2.29	1	0.81
		CETO	5.61	2.29	1	0.73
		CYMOPOLEIA	8.17	2.29	1	0.92
		LIR	5.60	2.29	1	0.94
	North lower	AHTI	5.10	2.01	1	0.64
11	Alcorn upper	POSEIDON	4.59	2.15	1	0.81
	Middle lower	NEPTUNE	--	--	2	--
	Middle upper	BRIZO	7.15	2.29	1	0.81
		CETO	5.61	2.15	1	0.64
		CYMOPOLEIA	8.68	2.29	1	0.99
		NEREUS	--	--	1	--
12	Alcorn upper	AHTI	2.55	2.42	2	0.56
		POSEIDON	5.61	2.29	1	1.06
	Middle upper	BRIZO	6.64	2.29	1	0.74
		CETO	8.16	2.42	1	0.95
		CYMOPOLEIA	8.68	2.42	1	1.00
		GALENE	--	--	1	--
		LIR	6.11	2.29	1	0.72
		NEREUS	--	--	1	--
		TIALOC	8.16	2.29	1	0.95
13	Middle upper	GALENE	--	--	1	--
		TIALOC	7.65	2.56	1	0.94
16	Middle upper	CYMOPOLEIA	7.66	2.56	1	0.82
		NEREUS	--	--	1	--
22	Middle lower	NEREUS	--	--	1	--
23	Middle lower	NEPTUNE	--	--	1	--
		NEREUS	--	--	1	--
	Grand Total			3.93	1.42	31

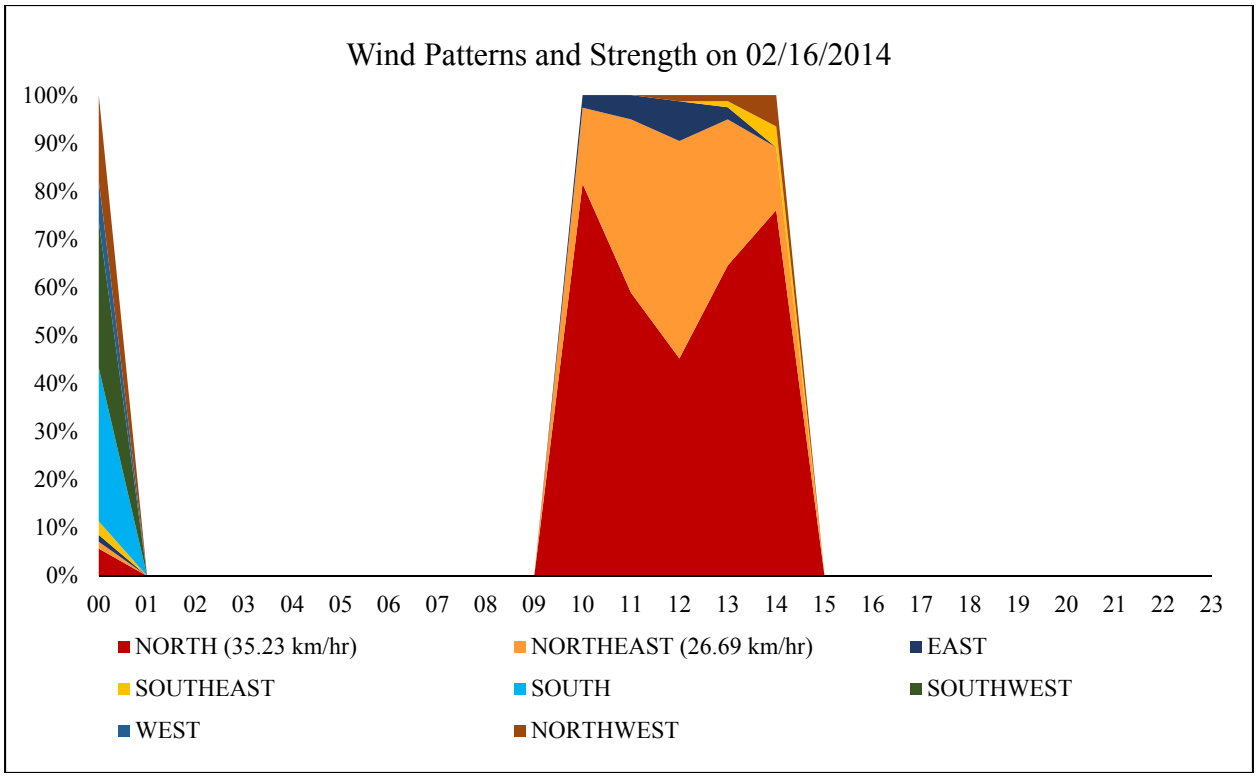

Figure 98. Wind Direction and Strength on February 16, 2014

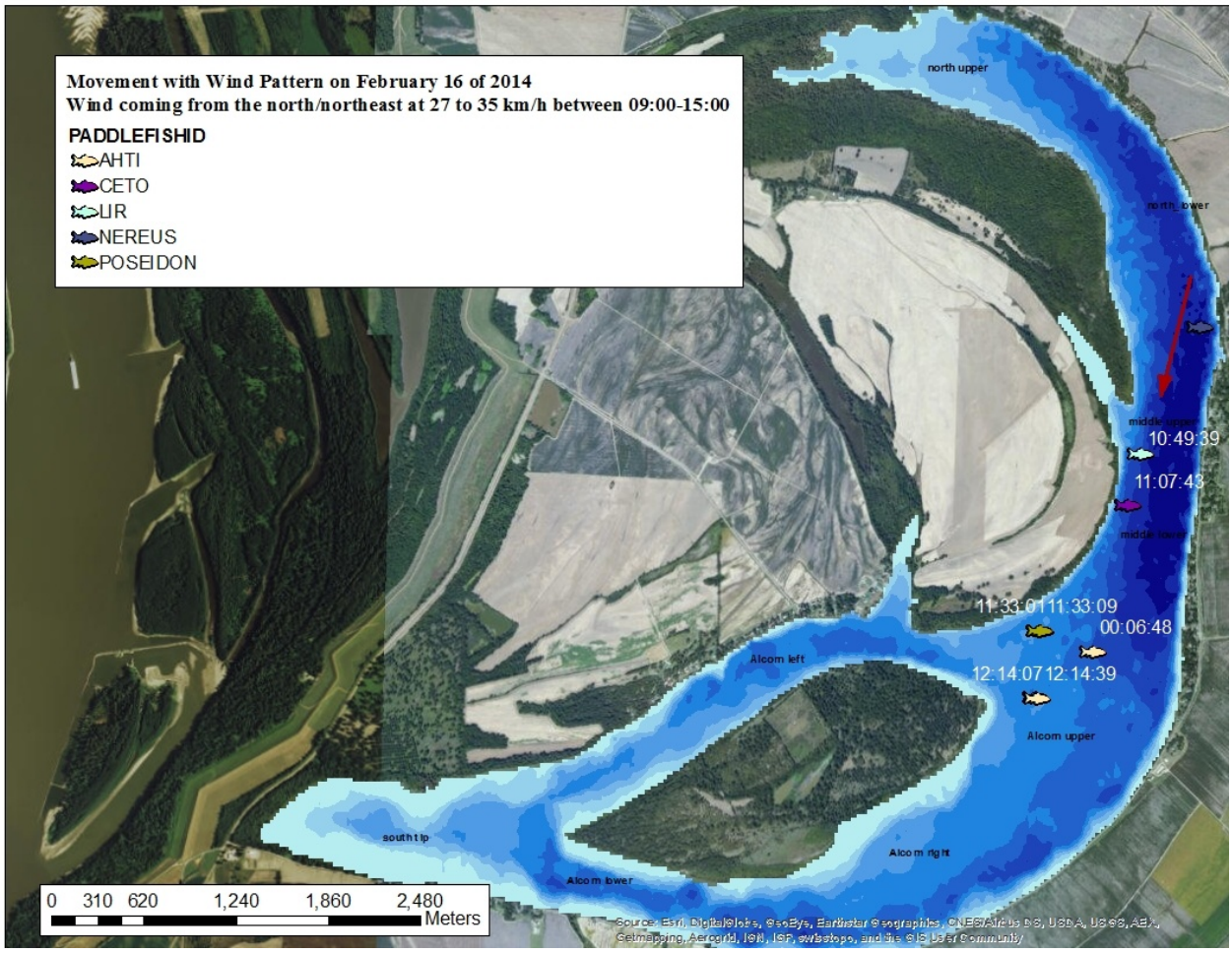

Figure 99. Movement with Weather Patterns on February 16, 2014

Table 37. Average density and calories per cubic meter for zooplankton samples taken at fish and random localities on February 16, 2014

DATE_	TIME_	Lake Section	Waypoint ID	Avg. Calories (m3)	No. of Tows	Avg. Density (no.org/m)
16-Feb	00:02	Middle lower	Random	72.24	1	--
	10:26	Middle upper	Nereus	78.58	1	1847.85
	10:52	Middle lower	Lir	84.62	1	4715.50
	11:09	Middle lower	Ceto	63.07	1	5135.09
	11:35	Alcorn upper	Poseidon	2	1	--
	12:16	Alcorn upper	Ahti	72.93	1	2347.11
	12:57	Alcorn right	Random	49.97	1	--
	13:34	Alcorn lower	Random	60.34	1	1028.67
	13:53	Alcorn lower	Random	265.39	1	3355.04
Grand Total				94.92	9	2047.70

Table 38. Movement, depths, and temperature of paddlefish on February 16 of 2014

Hour	Lake Section	Paddlefish ID	Avg. Fish Depth	Avg. Fish Temp	No. Locations	%Water Column
00	Alcorn upper	AHTI	3.57	2.70	1	0.00
10	Middle lower	LIR	5.60	2.70	1	0.86
	Middle upper	NEREUS	0.00	0.00	1	0.00
11	Alcorn upper	POSEIDON	3.06	2.83	2	0.69
	Middle lower	CETO	6.12	2.83	1	0.93
12	Alcorn upper	AHTI	3.57	2.83	2	0.77
	Grand Total		3.57	2.44	8	0.59

zooplankton were as high as 265.39 calories per cubic meter. On the east side of the Island again the zooplankton measures were (1,028 org/m^3 and 65 cal/m^3).

Movements on the February 16 were to the south/southwest in opposition to strong northerly winds (35 km/h). The following day on February 17 the winds began coming from the south (23 and 36 km/h) between 0500 and 1000 (Figure 100). The movement of fish began to shift to the north (Figure 101) which marked the beginning of the most extreme movement of paddlefish in response to wind direction occurring during this study. On February 23 persistent southerly winds (16.9 km/h) were concurrent with movement of paddlefish to the north sections (Figure 102). Fish movement progressively moved north and by February 23 nine of the ten fish were located in either north lower or north upper lake sections (Figure 103). Movements were also accompanied with a marked increase in temperature and a decrease in fish depth. Average fish temperature was 3.66°C at an average depth of 7.22 meters on February 17. Surface temperature averaged 2.58°C. On February 22 and 23 as fish swam north into shallower water (average fish depth: 3.5 meters) both surface and fish temperatures increased to 8.75 and 8.03°C, respectively.

4. Discussion

Foraging range is positively related to the renewal rate of the environment (Ford, 1983). A habitat with plentiful resources within close proximity is an efficient biological environment for ram-ventilating filter feeders such as paddlefish. Suspension feeding duration is directly proportional to prey availability. Paddlefish will suspension feed when prey concentrations are high enough to support activity. Winter movements in Moon Lake covered a narrow range with paddlefish spending the majority of time in the deepest sections of the lake. This is commonly found during winter residence. Paddlefish in stretches of the Missouri River overwintered in the

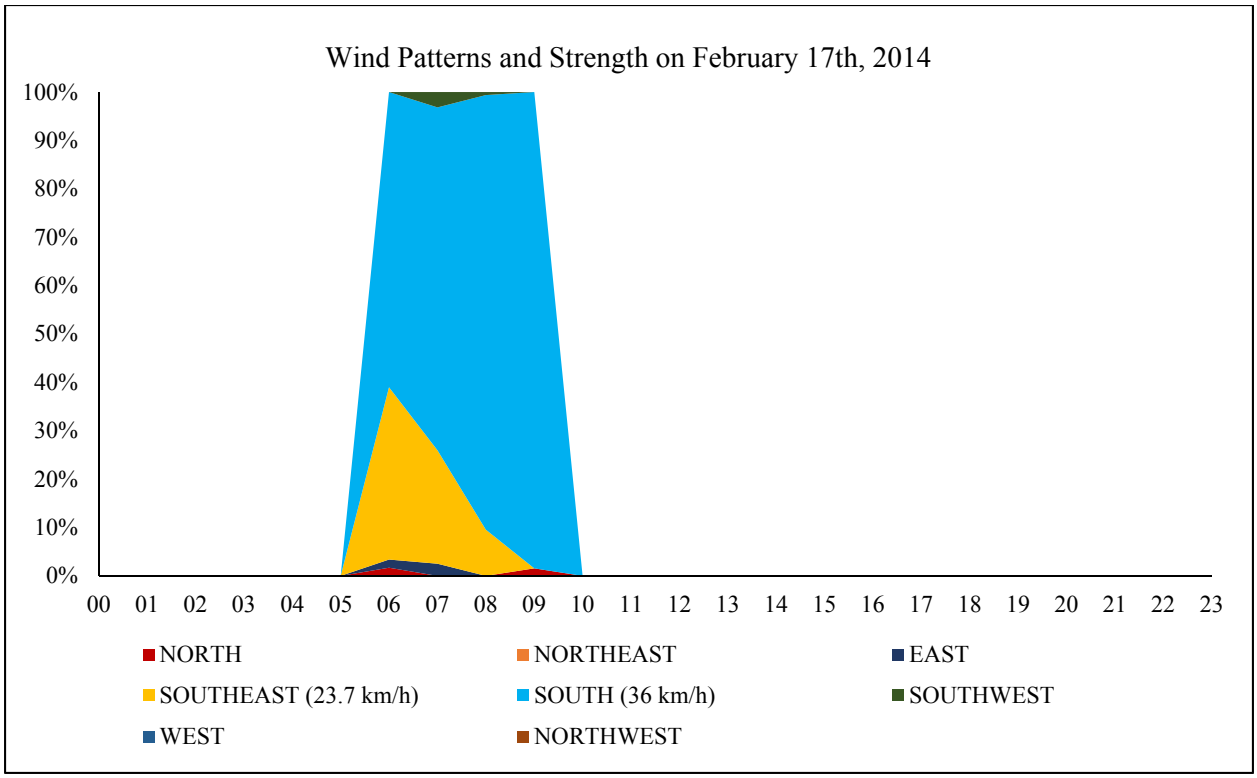

Figure 100. Wind Direction and Strength on February 17, 2014

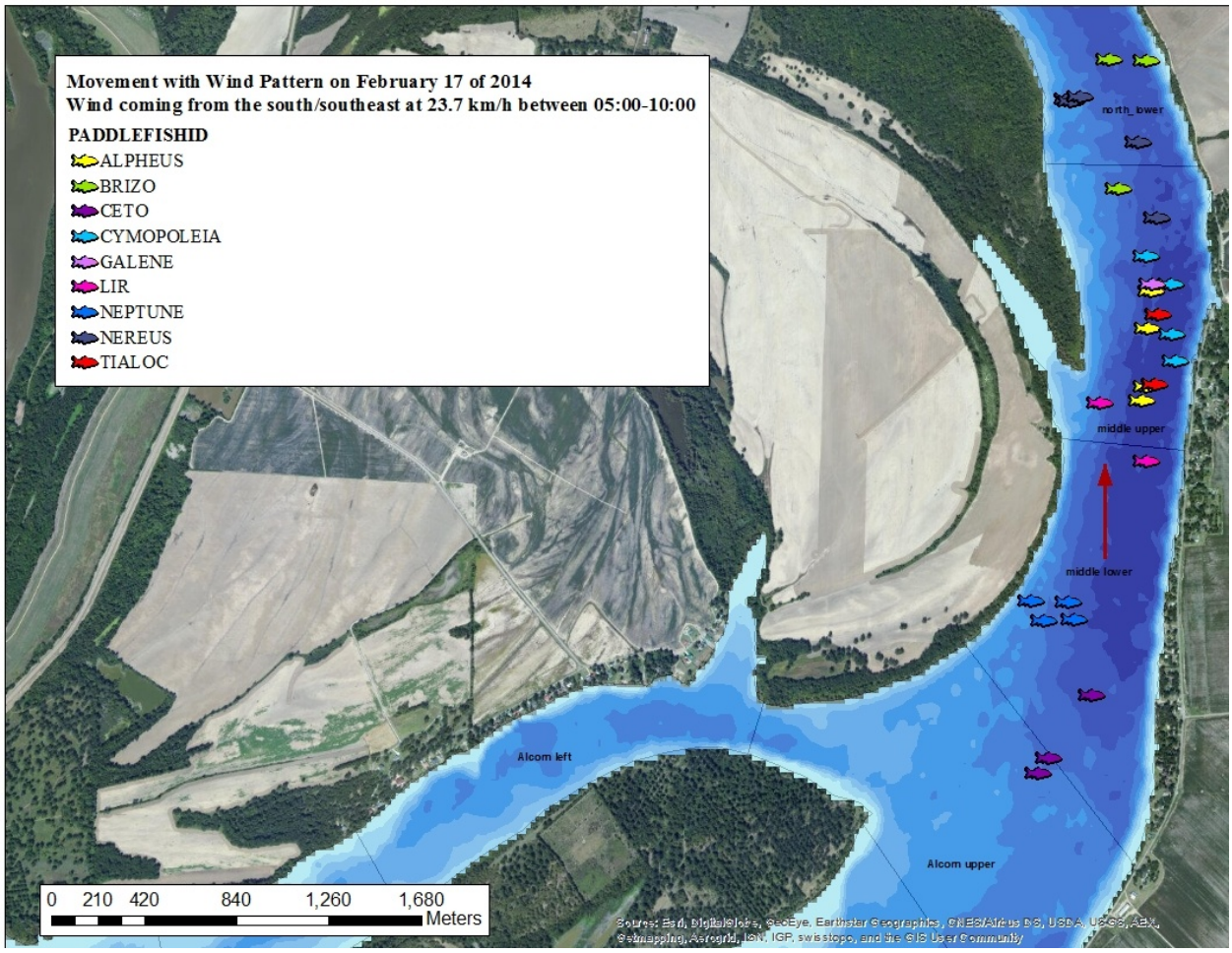

Figure 101. Movement with weather patterns on February 17, 2014

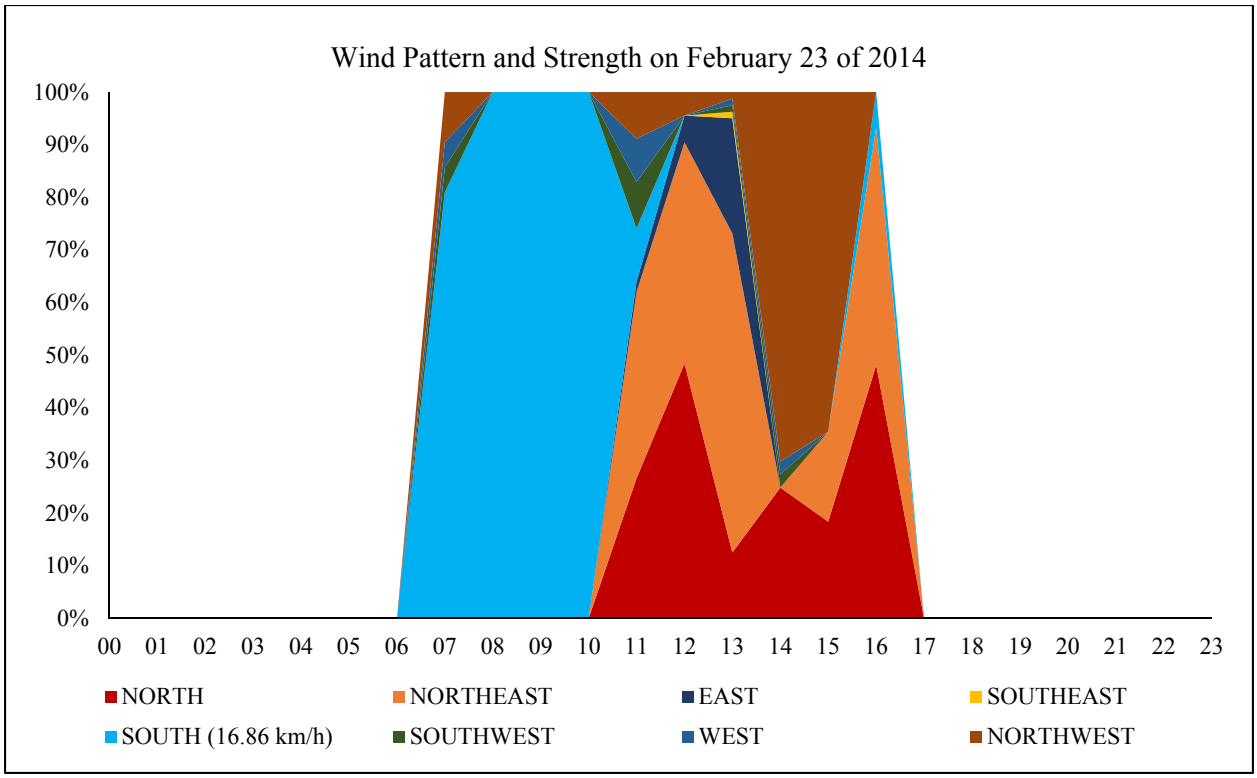

Figure 102. Wind Direction and Strength on February 23, 2014

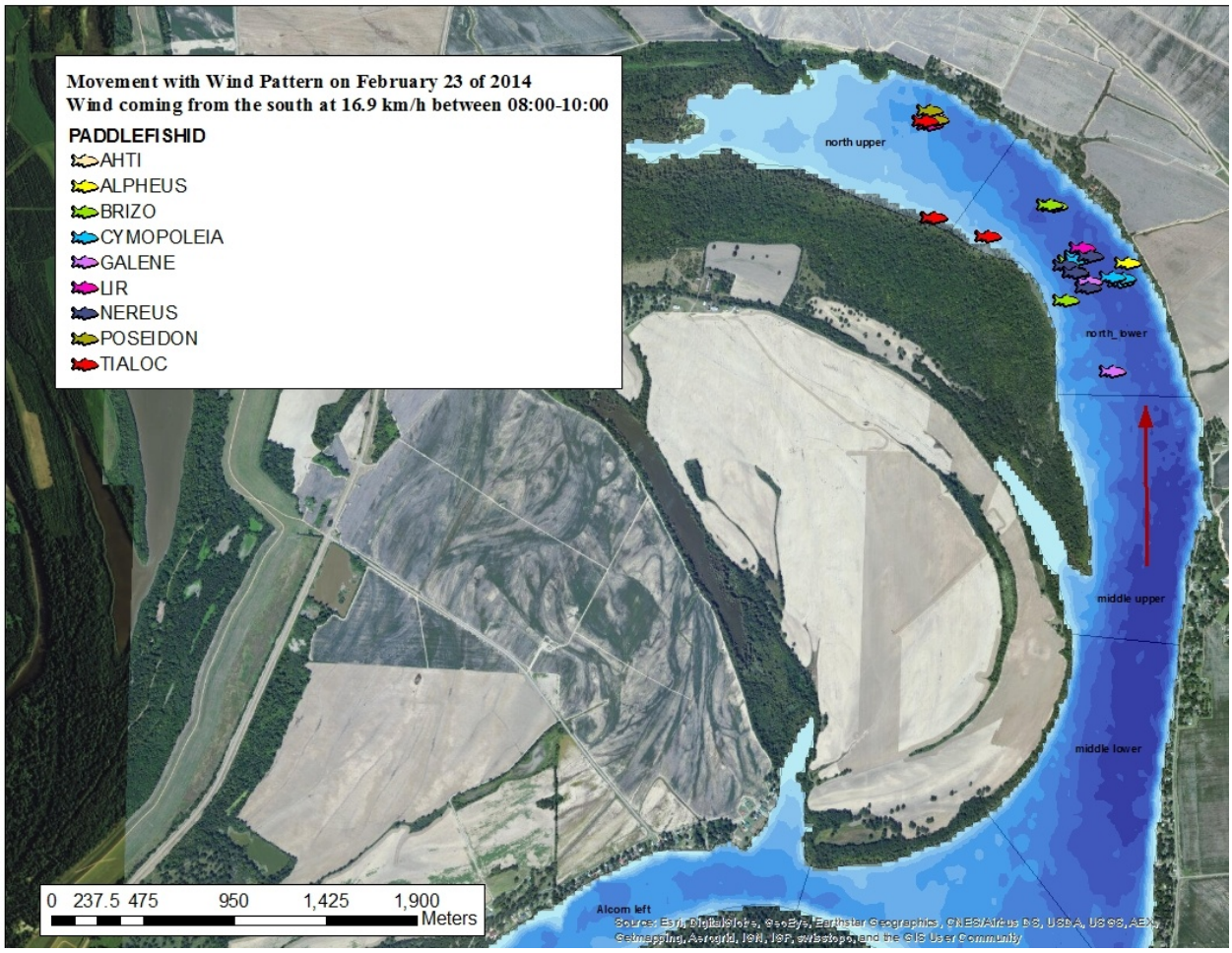

Figure 103. Movement with weather patterns on February 23, 2014

deepest pockets with the slowest currents (Rosen, 1976). It has been suggested that paddlefish feed very little during winter (Rosen and Hales, 1981) and that the optimal temperature for suspension feeding in paddlefish ranges between 7 – 20°C. The reduction in temperature decreases that rate of digestion and assimilation. Stomach evacuation can take in excess of seven hours (Rosen and Hales, 1981). The picture developing in Moon Lake is that the paddlefish remain in deeper waters swimming at speeds optimized for temperatures below 7°C. Cessation of suspension feeding is likely during periods of low zooplankton activity. However, warmer prevailing winds help to concentrate grazing zooplankton into pockets that make suspension feeding more efficient such that less time is spent acquiring more prey over a shorter period of time.

Seasonal residence in a highly productive environment such as Moon Lake presents a choice between "habitat-specific" profitability and reproductive potential among immature and reproductively developing paddlefish (Hoxmeier and Devries, 1997). For juvenile and young adult paddlefish, an energetic tradeoff exists between staying in a productive environment to continue to accrue energy reserves or to leave the lake and enter the reproductive population. As oxbows are not suitable spawning habitat paddlefish fish must leave to spawn (Jennings and Zigler, 2009). Leaving the oxbow too soon might decrease reproductive potential while remaining does not guarantee substantial reproductive growth. The benefits of feeding in oxbows is apparent. Paddlefish are much more robust than those from the main channel (Hoxmeier and Devries, 1997). Hoxmeier and Devries (1997) found that the condition factors of paddlefish (1.41±0.019) occupying Sibley Lake (Alabama oxbow) were significantly higher than paddlefish in the main channel (1.27±0.019). Moon Lake is an extremely productive lake as reflected in the average condition factor of the paddlefish found in this study (2.05±0.15 95% C.I.).

As the water levels rose during the spring, new areas were inundated causing an influx of detritus and other organic materials. Along with warmer temperatures zooplankton distribution increased laterally into shallower waters. The spring movements of paddlefish were much broader, covered more distance, and seemed to follow the zooplankton concentrations. The feeding peaks in March and April most likely coincided with elevated metabolic demands due to reproductive growth, development of lipid reserves (gonadal fat bodies), and rising costs of locomotion. Patterson et al. (2013) found that metabolic costs of routine swimming in paddlefish increased from 59.23 mg/O_2/kg/h to 202.52 mg/O_2/kg/h between 10 and 30°C (Patterson et al., 2013). In this study oxygen consumption rose from 71.43 to 152.02 mg/O_2/kg/h between November (15.6°C) and May (23.7°C) for fish weighing between 19.16 and 21.59 kg swimming at 76 cm/s. These results suggest that paddlefish increased search area to find adequate nutrient resources to effectively balance the rise in energetic demand.

In the winter the highest zooplankton densities and nutrient values clustered over a smaller area over deeper water. Eight-four percent of all winter locations were over the deeper sections of north lower, middle upper, and middle lower. The average caloric value of zooplankton in north lower, middle upper, and middle lower was 305 calories/m^3 for February. The average for north upper was 14 and the average for the bottom four sections, Alcorn upper, Alcorn left, Alcorn right, Alcorn lower, and south tip was 90 cal/m^3. During spring zooplankton abundance increased throughout that lake. Averages for March and April were 387 cal/m^3 in north upper, 178 in the middle sections, and 113 in the south. Zooplankton abundance dropped off precipitously in May with 42 cal/m^3 in the middle sections (winter range), and 156 in the southern sections. In September the numbers dwindled to less than 10 cal/m^3 across the entire lake. As zooplankton distribution expanded in the spring the paddlefish followed. Distribution of

paddlefish in the spring encompassed the entire lake and were equally represented over all periods of the day.

When considering foraging costs some key factors are important. A paddlefish will expend energy swimming between foraging areas. Sims (1999) reported that non-filter feeding basking sharks swim slightly faster than their theoretical swimming speeds predicted by Weihs (Weihs, 1975). Like its ram-filter feeding counterpart, paddlefish increase efficiency with swimming speed with the optimal swimming (U_{opt}) to be near 116 cm/s. Since time spent between foraging areas will only produce energetic losses it is a reasonable assumption that paddlefish would swim at U_{opt} between foraging sites to minimize the cost-to-benefit ratio. Reducing time spent searching would significantly reduce the energetic expenditure associated with daily activity. The distances necessary to travel between zooplankton patches is shorter during the winter. During the spring as metabolic costs rise and zooplankton distribution encompasses the entire lake, the time spent by paddlefish searching increases. Zooplankton abundance and distribution is a key factor affecting energetic expenditure associated with filter feeding in spring time conditions. Conducting a frequency time series of zooplankton distribution and dispersal in Moon Lake is thought for future research.

According to Hettler (1976), and James and Probyn (1989), the cost while suspension feeding is 1.75 times greater than while non-suspension feeding due to increased drag associated with swimming with the mouth agape. Sims (2000), reported that basking sharks reduced their swimming speed by as much as 24% when encountering increases in zooplankton densities. This reduction is likely a means to reduce swimming costs during filter feeding that are associated with increases in drag. Energy expended on locomotion would have several factors including cost of transport, zooplankton concentration, costs of suspension feeding, and costs associated

with cruising speeds while searching between foraging areas. For example, in February the difference in the cost of transport for a paddlefish swimming between 0.82 and 1.15 body lengths per second would be 0.0447 cal/g/km. The difference in the cost of transport for the same fish swimming in the spring would be 0.0903 cal/g/km. For a paddlefish weighing 25 kg it would cost an additional 2,257 calories to swim at 0.82 body lengths per second as opposed to swimming at 1.15 body lengths per second in the spring. The same fish swimming in February at 0.82 body lengths per second would only require 1,118 cal/g/km. A paddlefish with a mouth height of 16.09 and a mouth width of 17.98 would be able to filter 22.72 m^3 over one kilometer. The average calories per cubic meter of zooplankton patches sampled in the winter range was 305 cal/m^3. The theoretical number of calories gained through filter feeding in the winter is 6,929.6 calories per filtered kilometer for a fish weighing 25 kilograms and measuring 925 cm eye-to-fork length. Furthermore, a paddlefish weighing 25 kilograms and measuring an eye-to-fork length of 925 mm would expend between 0.1190 and 0.0743 calories per gram per kilometer during February swimming between 0.82 and 1.15 body lengths per second, respectively. If the paddlefish is cruising at U_{opt} while swimming between foraging sites and a 24% reduction in cruising speeds is accepted for this example, the fish would suspension feed at a swimming speed estimated around 86.6 cm/s (0.94 BLS). The cost of transport value at a swimming speed of 86.6 cm/s would be 0.108 cal/g/km. Applying an increase of 1.75 to simulate the elevated cost of foraging, the value would be 0.108 x 1.75 (0.189 cal/g/km) during February. The total cost in calories of suspension feeding over a distance of one kilometer would be 25,000 x 0.189 (4,725 calories). As calculated earlier a fish would gain an average of 6,929.60 calories per kilometer filtered while suspension feeding during February. This is a net gain of 2,204.60 calories. This estimate does not factor in the rate of zooplankton decline while suspension

feeding. With a net gain of 2,204.50 calories per kilometer a paddlefish would need to acquire in excess of the amount expended during searching. The importance of these variables will change with zooplankton abundance, dispersal, season, population size, and proximity to preferred habitat. It is assumed that paddlefish will spend energy returning to deeper waters after feeding and that the distance between this preferred habitat and the areas of zooplankton abundance will influence the distance traveled and expenditure associated with searching.

During February a paddlefish could swim slower over shorter distances and spend less energy given the zooplankton densities and caloric values found within their preferred habitat (north lower, middle upper, and middle lower). The caloric values in the upper and lower sections of the lake were on average lower than the caloric values within the winter area. Paddlefish would expend more energy traveling a further distance to receive fewer calories per distance while traveling outside of their winter habitat as opposed to foraging within. With less zooplankton and fewer calories available in areas outside of north lower, middle upper, and middle lower, it would be less efficient and likely, riskier to search and forage in these areas. Movement into these areas when they did occur were often accompanied with strong directional winds. On February 23, four fish were located together in north upper in an area of high zooplankton abundance (490 org/m^3) during strong, steady southerly winds (16.86 km/h). It is possible that any environmental factor such as prevailing winds that would facilitate paddlefish movement while promoting a more productive foraging area (pooling zooplankton concentrations) would be exploited by paddlefish as the situations arise.

5. Conclusions

This is one of the few studies that monitored the habitat use of paddlefish within an oxbow. Most studies were broader in scope looking at the diversity of habitat over a larger

geographical scale, such as that between oxbows lakes, backwaters, and main river channels. Paddlefish residence in Moon Lake occurred year round, but all paddlefish tagged in this study left the lake (or could not be relocated) between May and July with the majority leaving by May during periods of low zooplankton abundance. The sex and age of the fish in this study were not determined, but compared to other studies the population size was most similar to populations in Lake Pontchartrain, in Louisiana. Paddlefish do not spawn every year. Paddlefish were caught in Moon Lake from November 2012 to September 2014 suggesting paddlefish of different ages and sexual development use the lake year round in an attempt to increase fecundity. The rate of recrudescence slows with age and paddlefish that are not reproductive or energetically ready to spawn most likely delay leaving to increase reproductive potential. Some evidence has suggested that paddlefish return to Moon Lake. The first paddlefish caught in this study was last located April 25, 2013. It was thought to have left the area. However, it was caught the following year during the commercial harvest in February of 2014. This paddlefish was diminutive in size suggesting that it was a premature juvenile. Feeding peaked in spring during March and April when lake use was at its highest level. Compared to winter movements paddlefish in spring covered more distance over shorter periods and entered shallower waters more often. Likely, increased costs of reproductive development and increases in swimming expenditure were the impetus for elevated activity over a greater spatial scale.

CHAPTER V

A NEW DEVICE FOR MEASURING IN SITU SWIMMING SPEED IN THE AMERICAN PADDLEFISH, *POLYODON SPATHULA*

1. Introduction

Trefethen reported the first use of sonic electrical devices for the purpose of telemetric tracking of fish in 1956. Since then speed-sensing transmitters have been developed to measure swimming speeds and to estimate metabolic rates in a number of species including the blue marlin, *Makaira nigricans* (Block et al., 1992), the bonnethead shark, *Sphyrna tiburo* (Parsons and Carlson, 1998), the scalloped hammerhead shark, *Sphyrna lewini* (Lowe et al., 1998), and the lemon shark*, Negaprion brevirostris,* (Sundström and Gruber, 1998). These devices incorporate a moving pendulum, a spinning propeller, or a revolving paddlewheel to move a magnet past a reed-switch in a cyclical manner. The acoustic frequency transmitted from the opening and closing of the reed-switch is recorded and correlated to swim speed and oxygen consumption from prior laboratory swimming trials. The transmitters are attached to free-swimming wild fish for telemetric monitoring. Hydrophones are used to record the acoustic frequencies during manual tracking. These devices are relatively less expensive than other systems, such as electromyogram transmitters, (discussed below), but require continuous tracking and have a limited broadcast range. Transmissions range from a maximum of 4 kilometers in the transmitters used in the study by Block (1992) to less than 200 meters in the study by Lowe (1998). Battery life ranged from 6 to 21 days. The close proximity needed for

acoustic recordings is also a major drawback as it may interfere with normal behavior of fish in the study.

Over the last fifteen years electromyogram (EMG) transmitters have been a major way to estimate physiological parameters (swim speed, metabolic rate) of fish monitored in the field (Cooke et al., 2004). EMG transmitters are small surgical implants that are placed into the peritoneal cavity. Two wire leads are inserted into the lateral red muscle to measure the frequency and amplitude of muscle contractions. In the laboratory, fish are implanted with EMG transmitters and subjected to swimming trials over an appropriate range of swimming speeds. Typically, tail beat frequency, ventilation rate, oxygen consumption, and muscle contraction frequency and amplitude are measured and recorded. The relationship between metabolism, performance, and EMG output from laboratory trials are used to estimate energetic expenditure of locomotion of free-swimming fish in the wild. Cooke reported that nearly 60 studies using EMG technology have been conducted on 18 different fish species (Cooke et al., 2004) since 1990.

The major drawback of EMG methodology is the system requires invasive surgery and prolonged implantation of electrodes into the fish muscle. Retrieval of EMG transmitter data requires manual tracking which is time consuming, labor intensive, and may interfere or disrupt normal fish behavior. In smaller bodies of water a network array of fixed station receivers can substitute for manual tracking, but the arrays must be numerous to cover large areas. While this method may resolve many of the problems associated with manual tracking it comes with a higher monetary cost. Whether manual tracking or a network array is used, the signal sent from the transmitter is recorded and used to estimate swimming speed and metabolic performance using regression analysis.

Over the last decade advances in computer hardware, software, and social networking has provided a new platform for creative computing and invention. Programmers, electronic distributors, service providers, inventors, developers, and like-minded individuals, as well as, powerhouse companies such as Google, Apple, and Microsoft, have formed a community through social outlets to advance the creative spirit of electrical engineering and computer programming. The decline in component costs and the willingness of knowledgeable computer scientists and developers to share ideas, resources, tutorials, and technical support in an open-source format has led to a renaissance in electrical invention and device interconnectivity (The Internet of Things, IoT). People are using embedded microprocessors and the internet to network cost effective sensors that monitor, manage, and manipulate the world around them. The embedded microprocessor at the heart of such systems is readily available and easily programmable. The software or integrative development environments (IDE) are provided from the electrical manufacturers at no cost.

Arduino® is one of many electrical manufacturers of embedded microprocessors that provides a wide range of models that vary with technical needs and specifications. The Arduino® microprocessors are built using one of several Atmel microchips (Atmega 16U2, Atmega168) that control and communicate with sensors and peripheral devices through a series of digital input and output pins and buses.

In this study, a newly developed device is presented that circumvents some of the drawbacks of earlier speedometer designs. Unlike its predecessors, the electrical transduction is not manifest as an acoustic signal, but rather archived onto the tag itself as an electrical digital input. A 32,768 kHz crystal oscillator synchronizes time intervals with revolutions of a turning paddlewheel. The signal is transferred and recorded to internal read only memory that can later

be recovered and analyzed to estimate swimming speed of free-swimming fish. In this study the device and its components are described and a calibration curve is provided.

2. Materials and Methods

Components: Microprocessor, Memory, Time Clock, and Bluetooth

The microprocessor is an Arduino® Pro Mini 328 - 3.3V/8MHz from sparkfum.com. This board is based on the ATmega168 processor. The board is 18 x 33 x 0.8 mm and has 8 analog and 14 digital input/output pins. It has a FTDI chip for adapting serial to USB power and communication. It requires a 3.3V power supply and has an on-board voltage regulator for handling voltage supplies up to 12V. Voltage is supplied with a 3.7V 1000 mAh lithium ion battery connected to the JST power jack (Figure 104F) on a Bluefruit EZ-Link Bluetooth serial device. This bus provided an alternative power source for the microprocessor and provided a wireless connection via a virtual com port to a laptop or desktop computer for microprocessor programming.

A microSD breakout board (Figure 104H) was interfaced with the Arduino® Pro Mini microprocessor through a Serial Peripheral Interface (SPI) (Figure 105). The microSD dimensions are 31.85 x 25.4 x 3.75 mm and weighs 3.43 grams. A SanDisk Extreme PRO® microSDHC UHS-I card was used for non-volatile flash memory data storage. A ChronoDot real time clock (ChronoDot RTC) based on the DS3231 chip was connected to the microprocessor using an I^2C serial interface and powered with a CR1632 watch battery (Figure 104G). The ChronoDot RTC has a 30.4mm diameter, a height of 14.1 mm, and a weight of 4 grams (Figure 105).

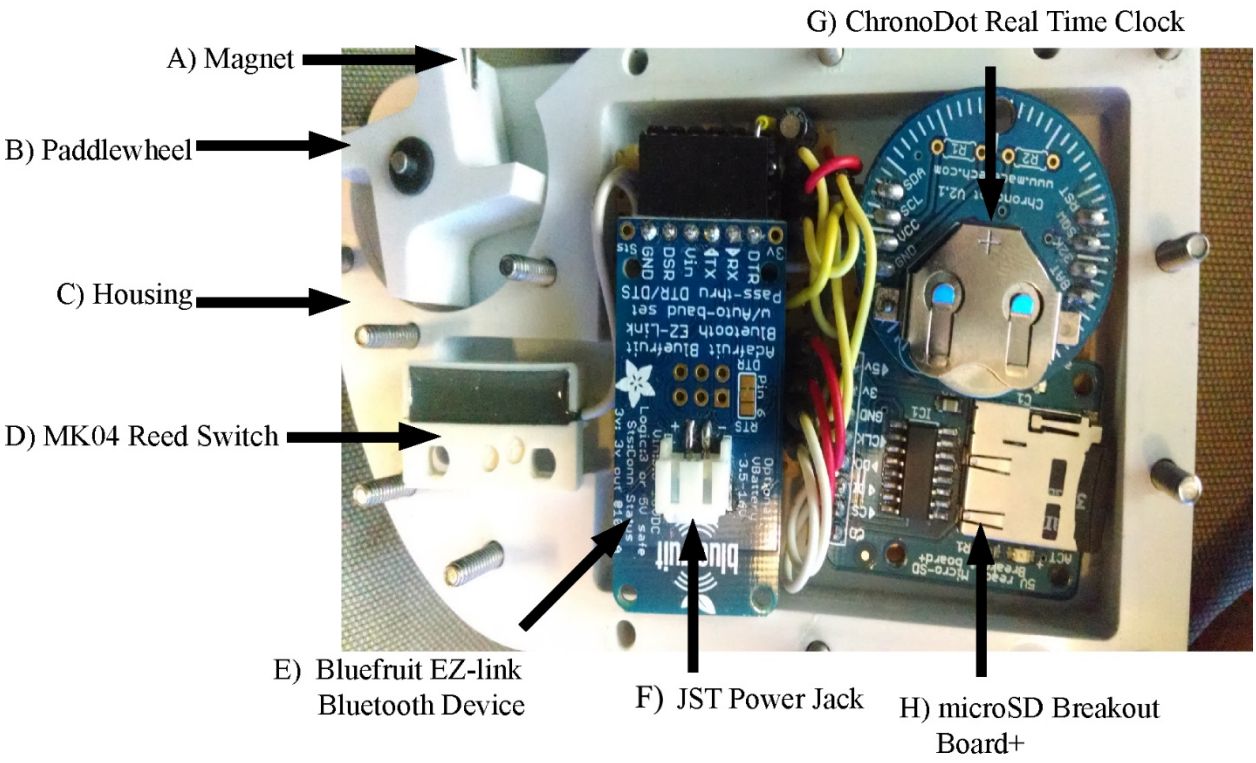

Figure 104. Ichthyometer housing, paddlewheel, and select circuitry. The Arduino® Pro Mini microprocessor is hidden under the Bluetooth device. A) rare-earth magnet, B) PVC paddlewheel, C) right half of PVC housing, D) MK04 reed switch, E) Bluefruit EZ-link Bluetooth, F) JST power jack for lithium battery attachment G) ChronoDot - ultra-precise real time clock - v2.1, H) micro SD card breakout board+. The Arduino® Pro Mini microprocessor is underneath the Bluefruit EZ-link Bluetooth Device. Refer to Figure 16 for more details.

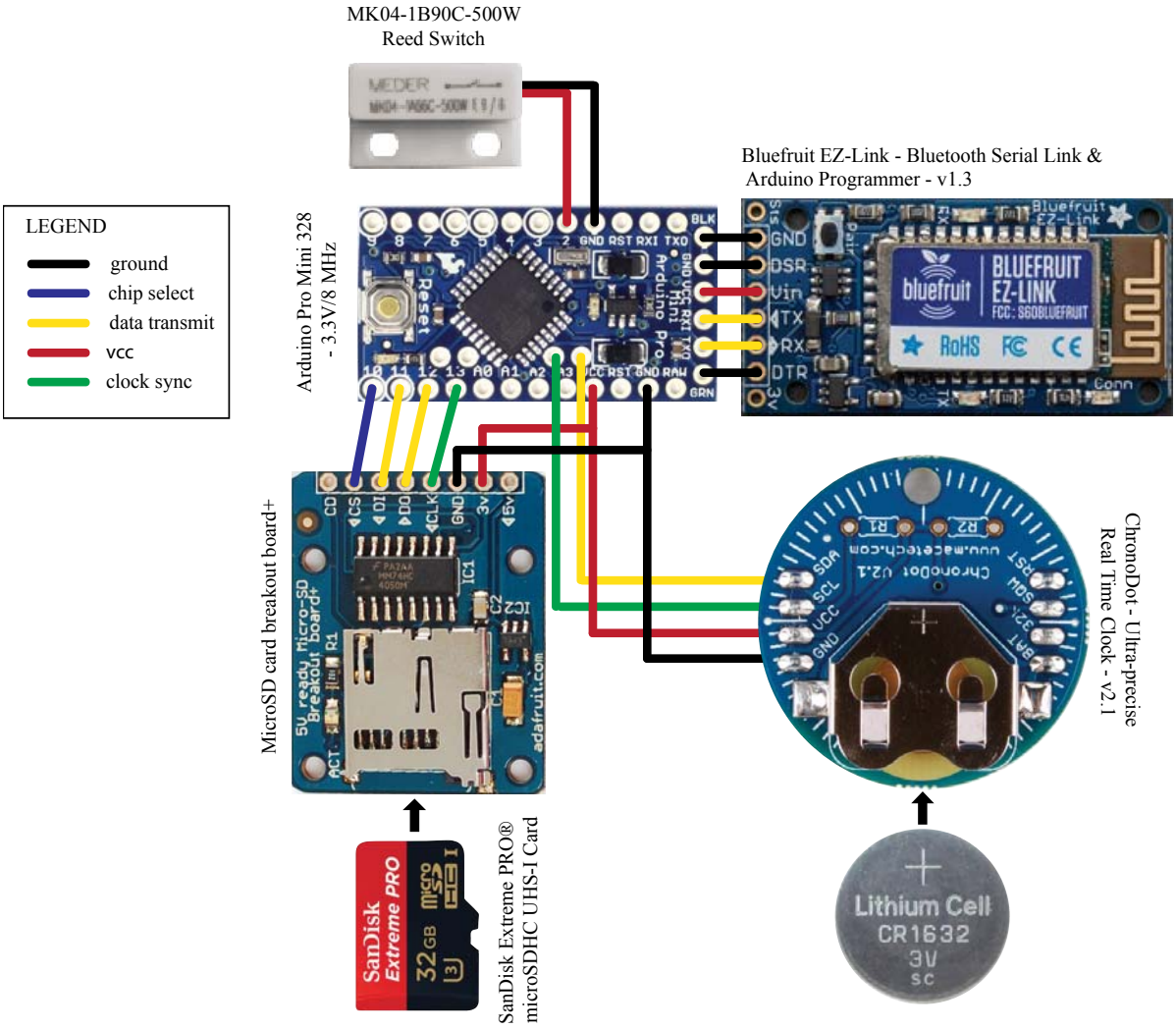

Figure 105. Electrical Components and Connections

Speedometer Housing

This section describes the materials and methods used to develop, build, and use a new speedometer device. The speedometer device, hereafter called the "ichthyometer" was composed of three main parts: 1) an outside housing (Figure 104C), 2) a free-spinning magnetic paddlewheel (Figure 104B), and 3) internal circuitry (Figure 105). The speedometer housing was a 116 x 69 x 24 mm box-shaped construction made of two halves of ½" PVC sheeting abutted to create two inner compartments and a single pocket in the lower corner of the apparatus. The two inner compartmental dimensions are 60 x 50 x 10 mm and 23 x 13.9 x 5.9 mm, house the microprocessor/sensors and the reed switch actuator, respectively. The housing was sealed with a 1/16" O-ring made of Buna-N cord (Figure 106), and 7/8" stainless steel socket hex screws and jam nuts. The O-ring was inset into a groove milled into the left halve of the housing to make a water-tight seal. A four-blade paddlewheel milled from the same material as the housing was suspended in the corner pocket by a metal dowel rod and spins freely in water flow (Figure 104B). A 1/8" rare earth magnet metal dowel and a 1/8" metal dowel weight were inserted into holes drilled into the long axis of odd blades (Figure 104A). These dowels offset the weight of the other dowel and promoted paddlewheel movement. A model MK04 reed switch from Standex-Meder Electrical Group was set in close proximity to the paddlewheel separated only by a thin compartmental wall (Figure 104D). The magnetized blade of the paddlewheel passes within actuation distance of the reed switch with each revolution. The total air weight of the speedometer was 204.9 grams. The housing was milled at the University of Mississippi, Center for Manufacturing Excellence.

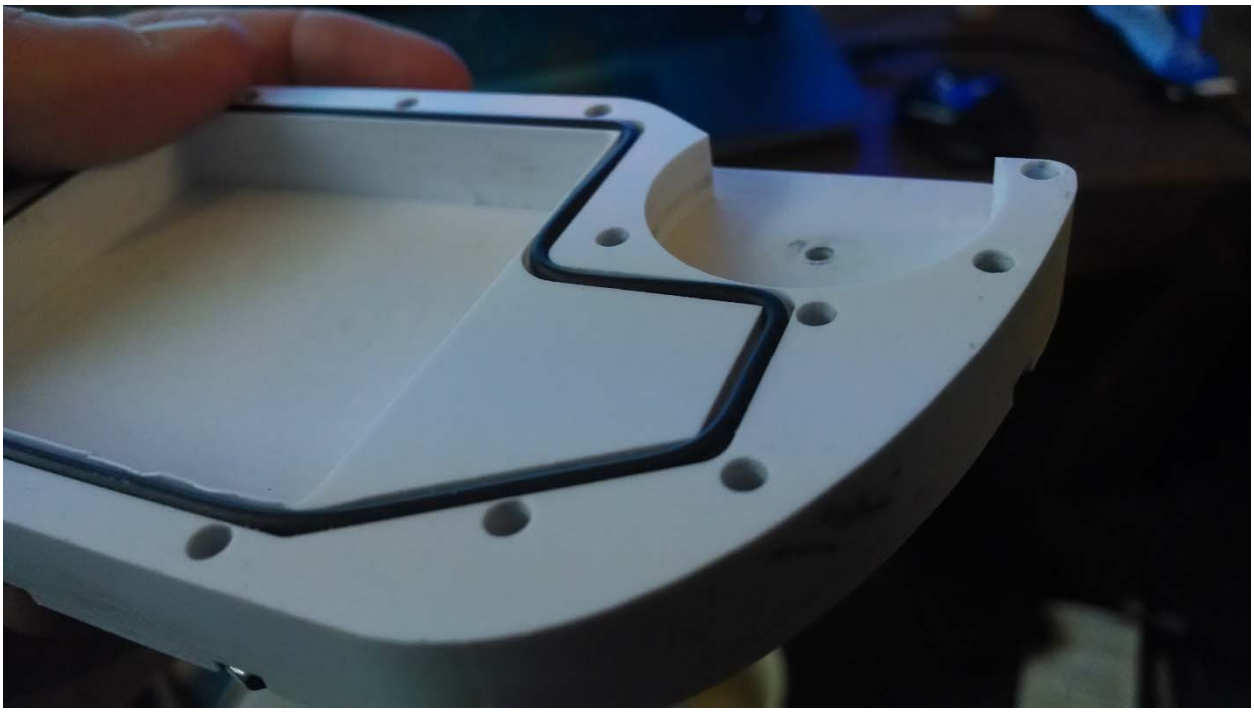

Figure 106. Left half of PVC housing and 1/16” O-ring made of Buna-N cord

Device Workflow

The speedometer generated a voltage frequency proportional to the revolutions of a paddlewheel spinning in flowing current. As a magnetic blade on a paddlewheel revolved past a MK04 Strandex-Meder reed switch, an electrical circuit to the Arduino® Pro Mini microprocessor was repeatedly opened and closed. The frequency was recorded to flash memory (32 GB SanDisk Extreme PRO® microSDHC UHS-I Card) as a timestamp generated from the ChronoDot RTC. A new record (example data: RPM: 1, 8/8/2014, 12:56:01) was added to a Microsoft Excel comma delimited file with each revolution. The regression equation ($Y = 0.0799 * X + 0.2104$) developed from the device calibration was used to estimate the water velocity in cm/s were Y is the water velocity (cm/s) and X is the average number of revolutions per 5 second interval.

Calibration

The correlation between water speed and paddlewheel revolutions was measured using a March-McBirney flowmeter. The speedometer and flowmeter head were attached to one end of a two foot metal pole and oriented perpendicular to its long axis and set parallel to one another. The flowmeter display and a stopwatch timer were fixed onto the dashboard of the boat and videoed during calibration. A timestamp generated by the speedometer was synchronized to the stopwatch timer before the start of calibration. Calibration was initiated by lowering the flowmeter and speedometer one meter beneath the water's surface and parallel to the water flow. The metal pole was fixed at a 90° angle by the side of the boat to assure that flow over the flowmeter sensor and paddlewheel were equivalent. Both the flowmeter sensor and paddlewheel of the speedometer were directly parallel with the water current direction. The boat was slowly motored forward for twenty minutes to generate and establish current. The speed was slowly

increased and decreased to subject the flowmeter and speedometer to a range of speeds between 0.66 and 2.25 meters per second. Calibration was performed in the calm water of the Yazoo Pass, an outlet of Moon Lake, on a day with little to no current.

Software and code

Programming the Arduino® Pro Mini microprocessor required the following: 1) setup hardware communication to a desktop or laptop computer via Bluetooth® wireless radio or wired USB, 2) the download and installation of the Arduino® integrated development environment (IDE), 3) the installation of the hardware drivers, 4) the import of libraries for peripheral device communications, 5) microSD card preparation, and 6) microprocessor programming.

Connection between the microprocessor and laptop was established via wireless radio transmission using a Bluefruit EZ-Link - Bluetooth Serial Link & Arduino® Programmer - v1.3 through a six-pin header (Figure 105). Power was supplied with a 1000 mAh lithium ion battery connected to the JST power jack on the Bluetooth device. A tutorial for adding the Bluefruit EZ-Link - Bluetooth Serial Link & Arduino® Programmer - v1.3 to a computer can be found at: https://learn.adafruit.com/introducing-bluefruit-ez-link. The integrated development environment (IDE) can be downloaded from the Arduino® website at http://Arduino®.cc/en/Main/Software. The programming language for Arduino® microprocessor is a derivative of the C++ programming language (Arduino® C). Instructional code was written in the integrated development environment (IDE) and sent to the microprocessor via a serial connection. The code provided in Appendix A should be copied and pasted over the default code that is present at the IDE startup (Figure 107).

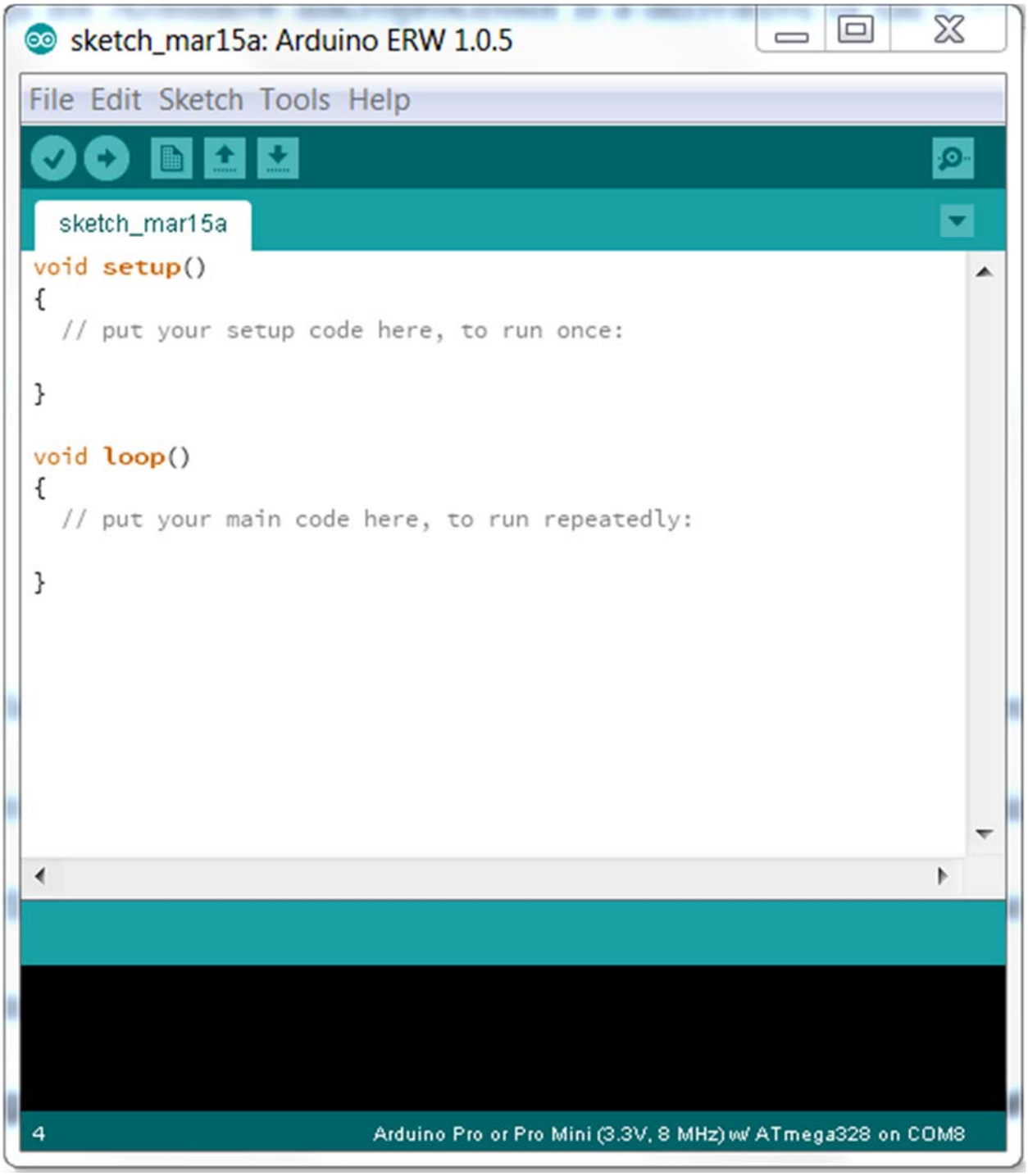

Figure 107. The Arduino® Integrated Development Environment

Libraries are folders of additional files that are located in the Arduino® library directory and contain two file types: header files and source files. The first four lines of code from Appendix A have "#include" statements:

```
#include <SD.h> //For talking to SD card
#include <Wire.h> //For RTC
#include "RTClib.h"
#include <SPI.h>
```

Include statements (#include <[headerfilename.h] >) provide any subsequent code access to the functions and definitions provided in header files. In the C++ programming language header files (denoted by the ".h") are additional code that add functionality to your program. These four lines of code provide access to four header files, SD.h, Wire.h, RTClib.h, and SPI.h, each from their respectively libraries. To save space and clarify readability, the include statements (#include <[headerfilename.h]>) capture the content of the header files and places it as if it were hard written at that line of code. The insertion of these #include statements act just as if the entire header file was inserted in its place. The SD.h, Wire.h, and SPI.h header files are default libraries installed in the Arduino® library subdirectory during the Arduino® IDE installation. The RTClib.h is a third-party library that must be downloaded and placed into the Arduino® library subdirectory. The header file that is a part of the RTClib library provides the functionality for communicating and programming of the ChronoDot RTC. The library folder (RTClib) must be downloaded and added into the Arduino® libraries subdirectory before compilation. The RTClib library can be downloaded from: https://github.com/adafruit/RTClib. To download and install this library (which includes RTClib.h header and RTClib.ccp source files), follow the link above. Click the "download zip" icon in the lower right corner of the website page (Figure 108 – arrow). After downloading is complete, copy the RTClib-master folder and paste it into the Arduino®

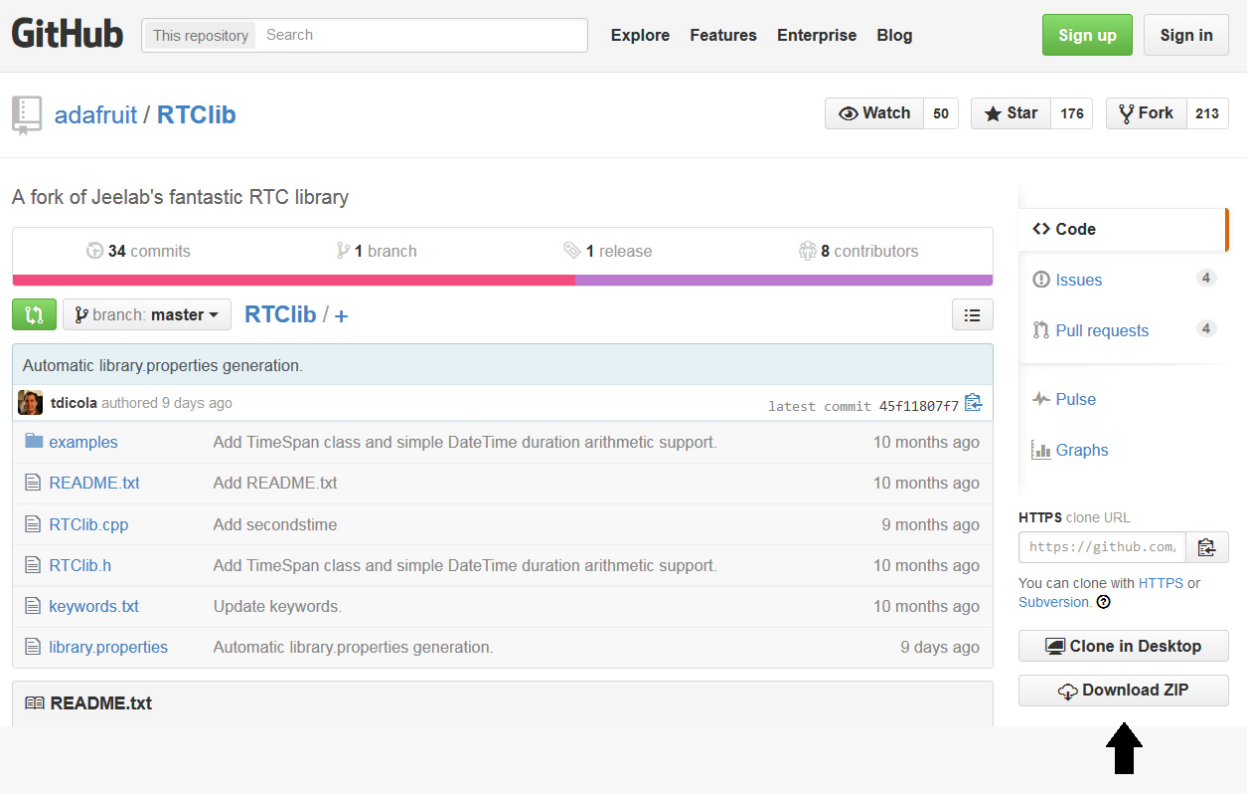

Figure 108. Screenshot of GitHub Repository for RTClib Library

library folder in the subdirectory that was created during Arduino® software installation. The path to the subdirectory library folder will depend on where the installation was placed, but follows the general form: C:\Program Files (x86)\Arduino®\libraries. Rename the folder "RTClib-master" to "RTClib" and place into the Arduino® library subfolder mentioned in the previous sentence. Once the RTClib library has been placed into the correct subdirectory the code in the IDE should verify and compile properly.

The program code uses a section block to configure the refresh rate. The refresh rate is a short delay, measured in milliseconds, that is used to prevent a system lockup. The numeric value for the refresh rate variable is stored in common text file. The text file will need to be created and saved onto the microSD card. Create this file using a basic text editor such as Notepad®. Do not use a rich-text editor such as Microsoft Word®. On the first line of the new file type the number "25" and save the file to the microSD card. Save the file using the filename "speed.txt". The filename must match the filename in the code. Anytime the refresh rate needs updating, the "speed.txt" file can be edited and resaved. Change the number "25" to any other number to increase or decrease the refresh rate and resave the file. No changes to the actual code are needed. The code opens the file, parses the number, and places the number in a variable called "refresh_rate". Place the microSD card into the microSD breakout board+.

All Arduino® C program code must be verified and compiled before uploading to the Arduino® board. To verify and compile click the circular icon containing a "checkmark" in its center (Figure 109A). Once the compilation is complete choose the correct board and COM port from the "Tools" dropdown menu. From the dropdown list select "Board", and scroll down and click on "Arduino® Pro or Pro Mini (3.3V, 8 MHz) w / Atmega 328". Next, choose the

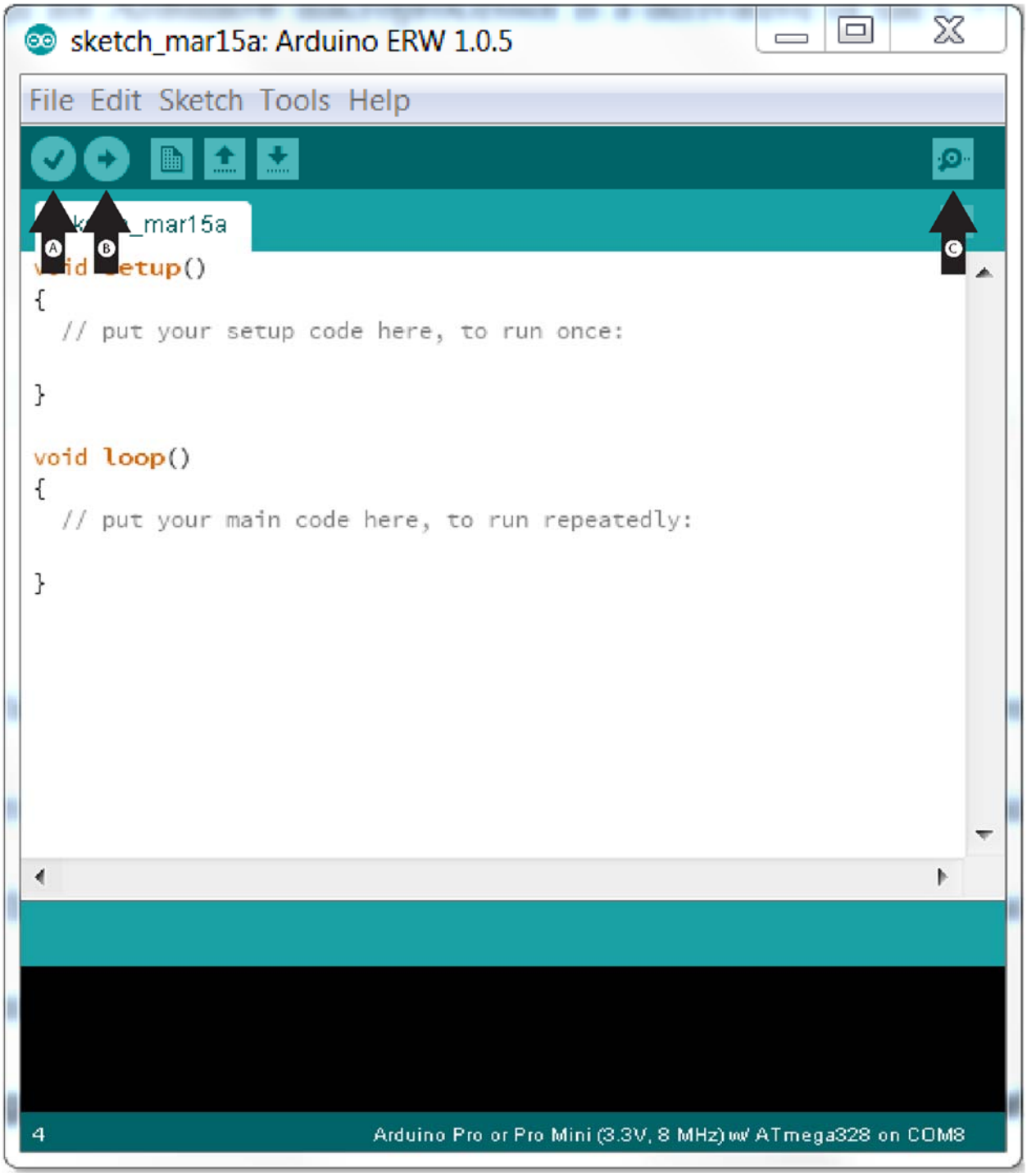

Figure 109. Verification and compiling.

appropriate COM port. To determine which COM port the Bluefruit EZ-Link - Bluetooth Serial device uses to communicate with the Arduino® board, open the control panel from the start menu of the laptop/desktop computer. Select “view devices and printers”. Right click on the EZ-link icon and select properties from the dropdown list. Select the “hardware” tab. The COM port will be noted next to the devices name. Back in the Arduino® IDE, from the “Tools” menu, select “Serial Port” from the dropdown list. Select the correct port. Once the correct board and COM port are selected in the Arduino® IDE, the program is ready to be uploaded to the microprocessor. Make sure power (lithium ion battery) is supplied to the EZ-link Bluetooth device via the JST jack. Upload the program by clicking on the circular icon containing a rightward facing arrow (Figure 109B). The LEDs on the EZ-link will begin to blink and flicker indicating data transfer. Following a successful upload the message “Done Uploading” will appear on the lower panel of the IDE.

Once the program is uploaded the programming of the microprocessor is complete. To test the functionality, click on the serial monitor icon (square with a magnifying glass centered in the middle). The icon is in the upper right corner of the IDE (Figure 109C). The serial monitor will open and a universal asynchronous receive transmit (UART) connection will be established between the laptop/desktop computer and the Arduino® board. The LEDs on the EZ-link will switch from blinking every few seconds to every other second to indicate a COM port connection has been established. The board will run an initial diagnostics test on the microSD card and printout the results to the serial monitor console window along with the current refresh rate from the “speed.txt” file on the microSD card (Figure 110). To test the reed switch functionality pass a small rare-earth magnet close to the reed switch. If the system is working properly a timestamp is printed to the serial monitor window (Figure 110). When the magnet

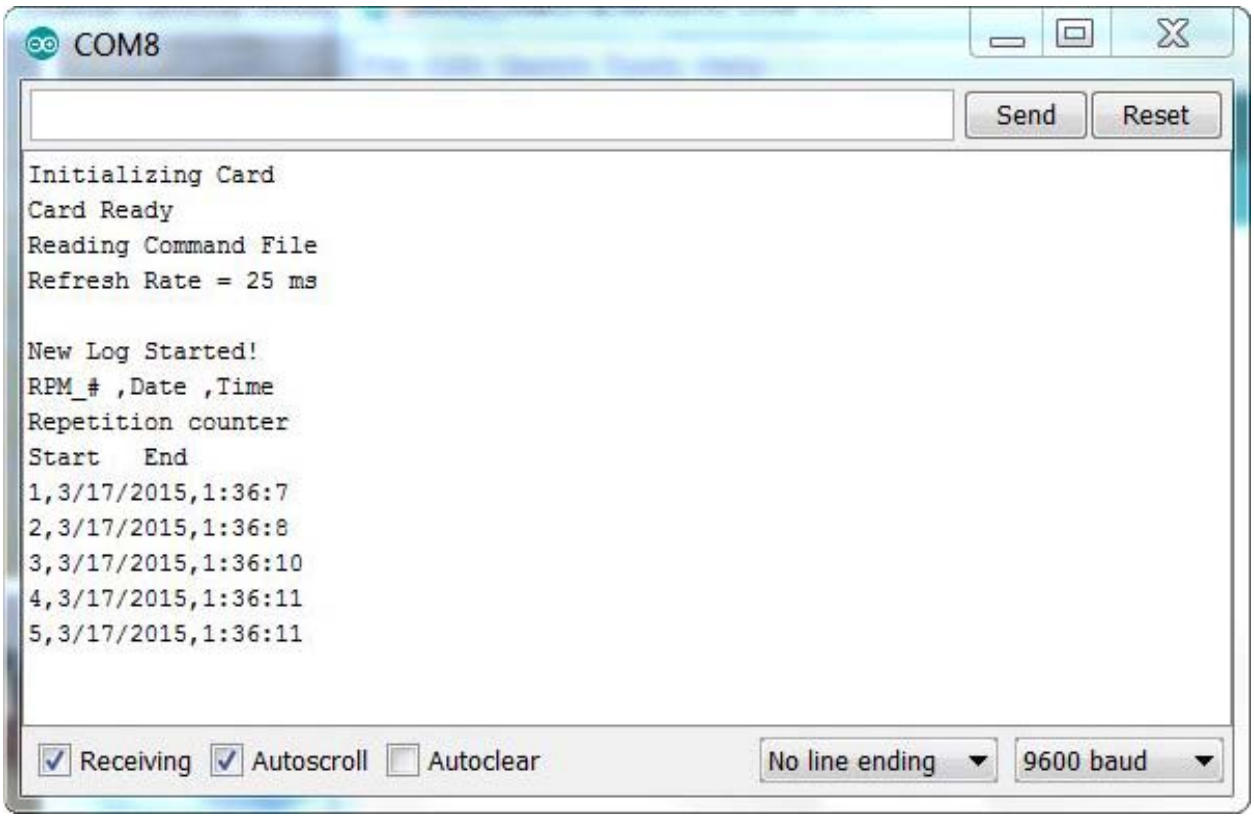

Figure 110. Testing ichthyometer functionality through the serial monitor window

closes the reed switch the electrical circuit is completed, the data output (the current number of revolutions and the current date and time) is sent to the serial monitor window, a timestamp is stored to a file named "log.csv", and the file is automatically created and saved to the microSD card.

Application

The ichthyometer, a radio transmitter (F2200 radio transmitter from Advanced Telemetry Systems), and a datalogger (LAT 1400 data logger from Lotek wireless®) were mounted using industrial strength cable ties and 50lb monofilament line onto the dorsal area of three paddlefish on May 3, May 19, and September 1, 2014, respectively (Figure 111). Using the acoustic radio signals from the transmitters, each fish was tracked by boat. Fish coordinates were recorded in decimal degrees using a handheld Garmin Rino 655t and a Garmin echoMap50 chart plotter and transferred into Microsoft Excel®. Locations were plotted using ArcGis® software. The fish tagged in early May was located 35 times between May 3 and May 19, 2014. The fish was recaptured using gill nets on May 19th, 2014. The Microsoft Excel data file was corrupted and no swimming speed estimates were possible. The fish tagged on May 19, 2014 remained in Moon Lake approximately 1 week before departing the lake. The speedometer was never retrieved. The fish tagged on September 10, 2014 was located a total of 25 times between September 10th and September 21st before the ichthyometer and transmitters became detached from the fish. The speedometer was never retrieved.

3. Results

A linear regression analysis established that the number of revolutions significantly predicted water speed (cm/s), F (1, 83) = 382.37, $p < 0.0013$, and that the number of revolutions accounted for 82.2% (r^2) of the explained variability in water speed (cm/s). The regression

Figure 111. Ichthyometer

equation was: Y = 0.210 + 0.08*X, where Y equals the predicted water speed (cm/s) and X equals the number of revolutions occurring every 5 seconds (Figure 112).

4. Discussion

The purpose of the ichthyometer was to measure and quantify the swimming speed and behavior of free-swimming paddlefish. The general objectives were: 1) to determine how paddlefish might exploit favorable conditions as swimming performance changes, 2) to determine if paddlefish shift swimming speed relative to prey abundance in order to optimize the ratio of swimming costs to energy intake, 3) to determine if swimming strategies change with seasonal increases in a paddlefish's scope of activity, and 4) to determine if environmental factors that decrease swimming performance pose a limit to the beneficial effects of increasing prey abundance. These were just a few questions that would have been addressed if the retrieval of the ichthyometer would have been successful and the data on microSD cards viable.

Calculating distance and speed of daily and seasonal movements may have provided estimates of the energy expenditure associated with locomotion and a better understanding of the dynamics of the biotic and abiotic factors affecting swimming performance. A primary objective of this study was to determine how factors effecting swimming performance (i.e. swim speed, temperature) and prey abundance might alter swimming strategy and contribute to subtle shifts in a simple cost-to-benefit ratio. The monitoring of changes in swimming speed and performance relative to changes in temperature and prey abundance may have allowed researchers to understand the factors that contribute to the optimization of the cost-to-benefit ratio via changes in swimming speed, increases in prey abundance, or some combination of both. The use of this newly developed device, along with radio telemetry, may have provided information about the contribution of habitat use, energetics, and community interactions.

Regression of Paddlewheel Revolutions vs. Water Speed

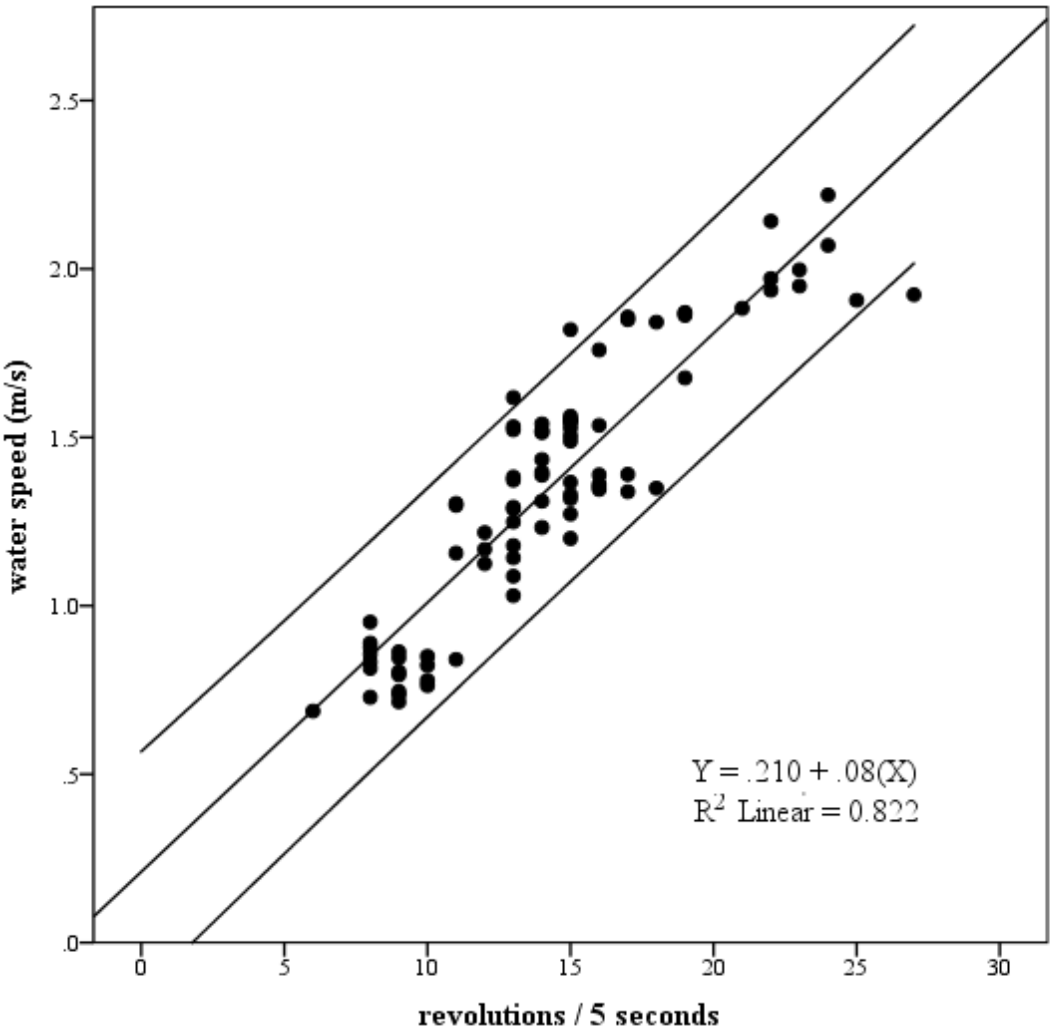

Figure 112. Regression of revolutions (#/5secs) versus water speed (m/s)

The ichthyometer had both added advantages and obvious problems over other similar techniques. The most important benefit was autonomy. Since data were recorded to computer memory the device was autonomous. Exposure to human interactions associated with manual tracking was limited, and the associated monetary and scheduling costs of fieldwork were offset. Along with a low price tag of $96.72 (Table 39) per unit the total operational costs was relatively low compared with other devices. This can be hugely beneficial to smaller budgets often associated with undergraduate and graduate research. However, autonomy had a major drawback: data retrieval was dependent on fish recapture and success was not achieved in this study. In addition, the method of attachment was more invasive than desired and the equipment may become detached prematurely from the paddlefish.

The design of the device was specific for this study and requirements may change with environment or organism studied and is considered a working prototype. Fish that reside in larger basins, periodically migrate over great distances, or spend time at depth, may not be suitable for study with this device. The device must be retrieved and larger lakes or marine habitats may be too large an area for tracking and recapture. Borrowing techniques from satellite pop-up tag technology may permit use in larger basins where recapture success is low. Modifications that allow a delayed detachment, much like the commonly used satellite pop-off tags, may be a viable solution. A satellite relay would transfer data once the device had reached the surface and satellite connection established.

Water quality is another consideration. The device was used in freshwater. Salt concentrations of marine and brackish environments were not tested. The O-ring system was designed to withstand depths of up to thirty feet in freshwater systems, but may not withstand the

Table 39. Component costs of the ichthyometer in US dollars

Component	USD
Arduino® Pro-Mini Microprocessor:	9.95
ChronoDot Real Time Clock (RTC):	17.50
MicroSD Breakout Board:	14.95
MK04 Reed Switch:	8.71
PVC Sheet Housing:	19.00
O-Ring:	0.11
EZ Bluetooth:	22.50
Neodymium magnet	1.00
Total Cost	$96.72

corrosive nature of seawater. It may be reasonable to assume that the stainless steel socket head screws and hex nuts that secure the housing would be sufficient.

5. Conclusions

Future development will attempt to consolidate components and extend battery life. Although the relative dimensions of the device are small in comparison to fish in this study (8.05 to 35.06 kilograms) it does pose a limitation to its use with smaller fish and diminutive species. Battery life is short lasting only a few days to a couple of weeks depending on temperature. Consolidating the computer chips and peripherals to a single PCB board and implementing code to incorporate a sleep mode will attempt to reduce the cost to the fish associated with the devices size and form factor, as well as, extend its operational life and data collection capabilities. Memory is not a limiting factor and is a significant advantage in this device. The microSD breakout board+ has a single microSD slot that can accept cards up to 128 GB providing significant storage that would likely outlast power supply.

An increase in metabolic expenditure associated with surgical stress, as well as, transport costs of carrying instrumentation (due to drag or tissue damage) may lead to underestimations of oxygen consumption due to locomotion. Laboratory tests swimming fish with and without speed-measuring devices may be a viable way to detect differences in swimming performance. The results might have provided suitable corrections factors to account for the differences in metabolic rates. The ratio of fish size to device weight may have been large enough to limit noticeable effects, but the technical difficulties of working with large paddlefish makes such efforts extraneous to the general objectives.

Careful consideration of the research goals is needed when incorporating this device into a research project. The hardware and software are flexible and may be modified to meet the

specifications of the research objectives. The reed sensor is just one of an endless number of sensors that can be attached to microprocessors. Temperature, infrared, pressure, light, and chemical sensors are just a few of the low cost sensors available. In combination, these sensors can record a multitude of data and data types. Nonetheless, the number of communication buses, the diversity of sensors, and the low cost make this technology a powerful tool for biological monitoring.

SIGNIFICANCE OF THE RESEARCH

Oxygen consumption rates have been measured in juvenile and sub-adult paddlefish, but consumption rates of adults have been missing from the literature (Burggren and Bemis, 1992; Xu et al., 2009; Patterson et al., 2013; Aboagye and Allen, 2014). This was due in large part to the lack of a swim tunnel respirometer large enough to accommodate such large fish and to the logistical, biological, and physiology constraints associated with conducting swimming trials on a continuously active ram ventilating species. Consumption rates from twenty-six adult paddlefish ranging in size from 78 to 107.5 cm were estimated in this study and combined with data from relevant work to construct a regression analysis (Figure 113). The regression includes consumption rates during active swimming at a speed of 76.05 cm/s. The addition of these data significantly increased the r^2 value from 0.48 to 0.57 and fills a significant gap in the extant data. A thorough set of consumption rates were estimated over a range of swimming speeds from 53 to 121.72 centimeters per second. This covers a wide range of activity in adult paddlefish and can be used to generate bioenergetics models of paddlefish locomotion to be used in further research and fisheries management.

The researcher has developed an innovative way of measuring in-situ swimming speeds in free swimming paddlefish. This valuable data has allowed researchers to combine laboratory estimates of oxygen consumption rates with real-world paddlefish activity. This new technology has provided researchers with more accurate information for understanding paddlefish swimming performance and behavior. The device is open sourced and inexpensive. This allows future

researchers and developers to modify and enhance the prototype for use with their research or to come up with new and innovative ways to expand its applications.

Oxbows and backwaters habitats are important seasonal residences for the American paddlefish. These habitats promote somatic and reproductive growth before spring migrations. This research provided important underlying factors influencing the dynamic relationship of habitat use, swimming performance, and prey abundance that will be useful for understanding paddlefish bioenergetics. This information lays a strong foundation for future research in areas of carrying capacity, swimming performance, energetics, migrations, and optimal foraging. Additional research is needed with respect to the relationship of zooplankton abundance, distribution, and nutrient values within these systems. Likewise, increasing sample sizes of swimming trials over a wider range of swimming speeds and fish sizes would help strengthen results found in this study.

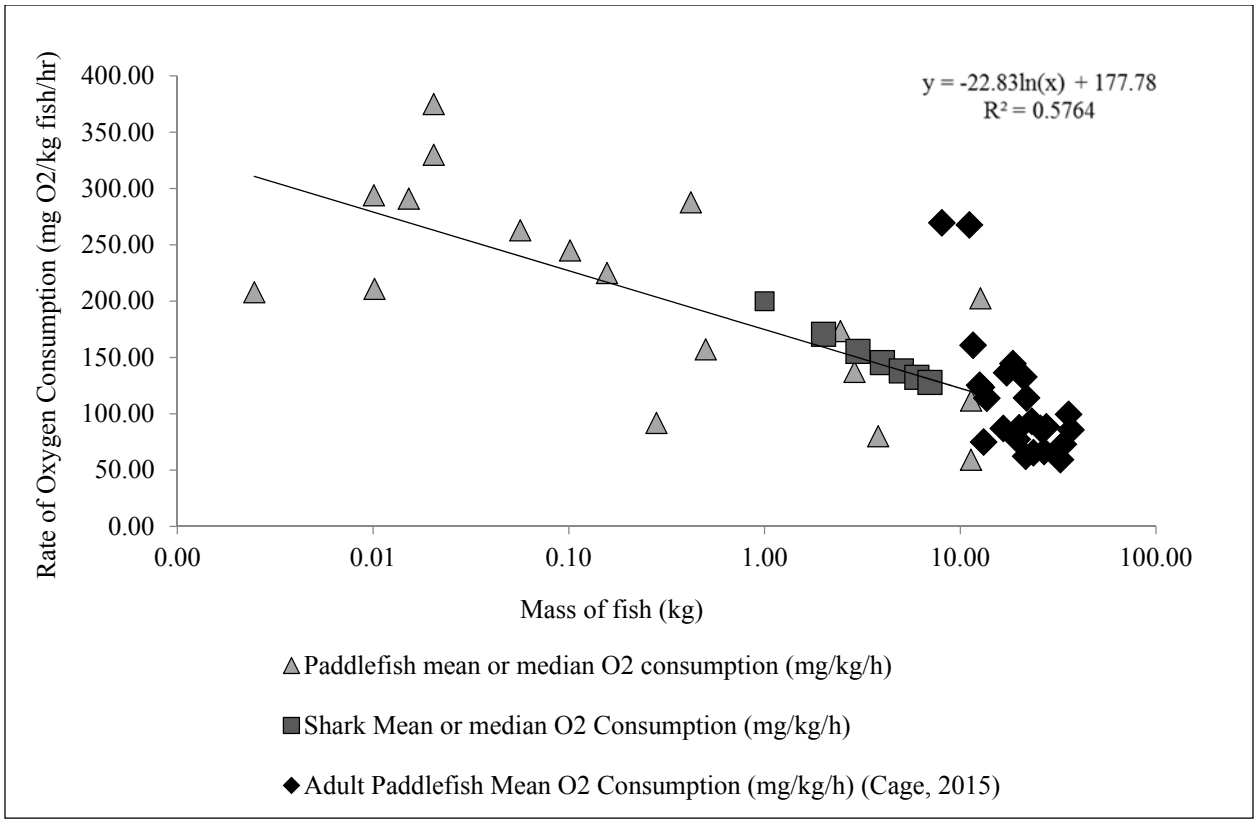

Figure 113. Oxygen consumption rate ($mgO_2/kg/h$) vs. fish mass (kg). Paddlefish mean or median O_2 consumption (Burggren and Bemis, 1992; Xu et al., 2009; Patterson et al., 2013; Aboagye and Allen, 2014), Shark mean or median O_2 consumption (Dowd et al., 2006). Adult paddlefish mean O_2 consumption (Cage, 2015).

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APPENDIX

Appendix A

Ichthyometer Programming Code

```
#include <SD.h> //For talking to SD card
#include <Wire.h> //For RTC
#include "RTClib.h" //This header file is included in the RTClib library found at
                            https://github.com/adafruit/RTClib
#include <SPI.h>//For talking to microSD breakout board+

//Define pins
//SD card is on standard SPI pins
//RTC is on Standard I2C Pins
const int CS_PIN      =10;
const int SD_POW_PIN  =8;
const int RTC_POW_PIN =A3;
const int RTC_GND_PIN =A2;

// Reed switch repetition counter
int sense0 = 2;
int sense1 = 3;
int counter0 = 0;
int counter1 = 0;
long lastDebounce0 = 0;
long lastDebounce1 = 0;
long debounceDelay = 50;      // Ignore bounces under 1/2 second

//Default rate of 5 seconds
int refresh_rate = 5000;

//Define an RTC object
RTC_DS1307 RTC;

//Initialize strings
String year, month, day, hour, minute, second, time, date;

void setup() {
  Serial.begin(9600);
  Serial.println(F("Initializing Card"));

  //CS pin, and pwr/gnd pins are outputs
  pinMode(CS_PIN,   OUTPUT);
  pinMode(SD_POW_PIN, OUTPUT);
  pinMode(RTC_POW_PIN, OUTPUT);
  pinMode(RTC_GND_PIN, OUTPUT);
```

```
//Setup power and ground pins for both modules
digitalWrite(SD_POW_PIN, HIGH);
digitalWrite(RTC_POW_PIN, HIGH);
digitalWrite(RTC_GND_PIN, LOW);

//Initiate the I2C bus and the RTC library
Wire.begin();
RTC.begin();

//If RTC is not running, set it to the computer's compile time
if (! RTC.isrunning())
{
  Serial.println(F("RTC is NOT running!"));
  RTC.adjust(DateTime(__DATE__, __TIME__));
}
 //Initialize SD card
if (!SD.begin(CS_PIN))
{
  Serial.println(F("Card Failure"));
  return;
}
Serial.println(F("Card Ready"));

//Read the configuration information (speed.txt)
File commandFile = SD.open("speed.txt");
if (commandFile)
{
  Serial.println(F("Reading Command File"));
    while(commandFile.available())
  {
    refresh_rate = commandFile.parseInt();
  }
  Serial.print(F("Refresh Rate = "));
  Serial. print(refresh_rate);
  Serial.println(F(" ms"));
  commandFile.close();
}
else
{
  Serial.println(F("Could not read command file."));
  return;
}
 //Write column headers
File dataFile = SD.open("log.csv", FILE_WRITE);
if (dataFile)
{
```

```
    dataFile.println(F("\nNew Log Started!"));
    dataFile.println(F("RPM_#,Date,Time"));
    dataFile.close(); //Data isn't actually written until we close the connection!

    //Print same thing to the screen for debugging
    Serial.println(F("\nNew Log Started!"));
    Serial.println(F("RPM_# ,Date ,Time "));
  }
  else
  {
    Serial.println(F("Couldn't open log file"));
  }
   pinMode(sense0, INPUT);
  digitalWrite(sense0, HIGH);
  pinMode(sense1, INPUT);
  digitalWrite(sense1, HIGH);
  attachInterrupt(0, trigger0, FALLING);
  attachInterrupt(1, trigger1, FALLING);
  Serial.println("Repetition counter");
  Serial.print("Start");
  Serial.print("\t");
  Serial.println("End");
}
void loop() {
  //Get the current date and time info and store in strings
  DateTime datetime = RTC.now();
  year  = String(datetime.year(),  DEC);
  month = String(datetime.month(), DEC);
  day  = String(datetime.day(),  DEC);
  hour  = String(datetime.hour(),  DEC);
  minute = String(datetime.minute(), DEC);
  second = String(datetime.second(), DEC);

  //Concatenate the strings into date and time
  date = month  + "/" + day + "/" + year;
  time = hour + ":" + minute + ":" + second;
  delay(refresh_rate);
}


void trigger0() {
  if( (millis() - lastDebounce0) > debounceDelay){
    counter0++;
     //Open a file and write to it.
  File dataFile = SD.open("log.csv", FILE_WRITE);
  if (dataFile)
```

```
  {
    dataFile.print(counter0);
    dataFile.print(F(","));
    dataFile.print(date);
    dataFile.print(F(","));
    dataFile.println(time);
    dataFile.close(); //Data isn't actually written until we close the connection!
  }
  else
  {
    Serial.println(F("Couldn't open log file"));
  }
    Serial.print(counter0);
    Serial.print(",");
    Serial.print(date);
    Serial.print(",");
    Serial.println(time);
    lastDebounce0 = millis();
  }
}
void trigger1() {
  if( (millis() - lastDebounce1) > debounceDelay){
    counter1++;
    lastDebounce1 = millis();
  }
```

VITA

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EDUCATION

Master of Science, University of Louisiana – Monroe **May 1999**
Monroe, LA

- Degree Area: Biological Sciences
- Concentrations: Systematics, Fish Evolution
- Thesis Title: A Review of the Spinycheek Sleepers, *Eleotris (Teleostei Eleotridae)* of the Eastern Pacific Basin
- GPA: 3.94

Bachelor of Science, University of Louisiana – Monroe **May 1996**
Monroe, LA

- Degree Area: Biological Sciences
- GPA: 2.84

PROFESSIONAL EXPERIENCE

Instructor, University of Mississippi **2011-2012**

- Courses: Human Anatomy and Physiology I & II
- Applied teaching skills to develop course syllabus, laboratory activities, lectures and exams
- Assisted students in understanding of course objectives including acquiring a working knowledge of the human body and anatomical terminology, and how body systems integrate to maintain homeostasis

Teaching Assistant, University of Mississippi **2011-2013; 2002-2006**

- Courses: Human Anatomy and Physiology I & II, Genetics, Introductory Biology for Majors I & II
- Supervisors: Dr. Carol Britson | 662.915.7988 | and Dr. Gail Stratton | 662.915.5786
- Prepared and conducted laboratory exercises and practical exams, provided weekly office hours and tutoring sessions, evaluated student work and maintained student grades
- Utilized the best methods of presenting and reinforcing new information to large groups
- Assessed the individual cognitive needs of the students and developed ways to aid in their education

Fisheries Technician, Idaho Fish and Game, Region 2 **2010-2011**

- Focuses: High Mountain Lakes Research Project & White Sturgeon Research Project
- Supervised a research team on a high mountain lake amphibian assessment project
- Managed and trained personnel on the TruDR lx digital radiography system (Sound-Eklin) to examine the number of hooks in the alimentary canal of white sturgeon (*Acipenser transmontanus*) in Idaho's Snake River
- Responsible for the inspection and routine maintenance scheduling for high mountain work vehicles
- Coordinated with local outfitters, US Forest service personnel, and IDFG crew members to plan and perform alpine research expeditions
- Ensured all field equipment was operational and organized to properly conduct field research
- Maintained databases, ran statistical analyses, and authored mid-term and end of year reports

Research Technician, University of Mississippi **2003-2006**

- Collected red snappers (*Lutjanus campechanus*) from artificial reefs in the Mississippi gulf and ensured appropriate transportation of the fish to the testing site
- Obtained behavioral, morphological, and physiological data used to evaluate swimming criteria and reaction to flow dynamics

Research and Field Technician, USDA Forest Service, Oxford, MS **2002**

- Performed seining and electrofishing to collect redfin darters (*Etheostoma whipplei*), orangethroat darters (*Etheostoma spectabile*) and rainbow darters (*Etheostoma caeruleum*) from the Tennessee and Tombigbee river basins
- Utilized stereology software and pertinent hardware to quantify egg diameter and developmental stage to determine female fecundity and to examine otolith rings to determine fish age

Research and Field Technician, Army Corps of Engineers, Vicksburg, MS **1997**

- Surveyed borrow pits to determine environmental characteristics that promote fish habitation and maximize species diversity
- Applied extensive knowledge of fish taxonomy to identify species found within the pit

Assistant Museum Curator, University of Louisiana – Monroe **1996-1999**

- Supported supervisors in all aspects of the fish and amphibian collection
- Aided in the maintenance of the museum acquisition database, designed and updated information cards, oversaw shipping and receiving, and conducted guided tours to elementary and high school students

Teaching Assistant, University of Louisiana - Monroe **1996-1999**

- Courses: Introduction to Biology, Introduction to Zoology